



Distinct responses of baseline and stress-induced corticosterone levels to genetic and environmental factors



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ABSTRACT

Glucocorticoid (GC) hormones, i.e. corticosterone (CORT) in birds, support physiological homeostasis and facilitate adaptations to stressful situations. However, maintaining high GC levels are energetically costly and interfere with other physiological processes. To keep the balance of costs and benefits of GC hormones, various mechanisms act to adapt GC levels to environmental conditions on different timescales, i.e. over generations, between parents and their offspring and within the life-time of a single individual. We elucidated whether two strains (domesticated and wild) of grey partridges (*Perdix perdix*) differed in the developmental trajectories of baseline and stress response CORT throughout the first 80 days of life. We also explored the potential of prenatal and postnatal factors, e.g. parental origin, predictable vs. unpredictable food treatments, individual and social factors to modify these trajectories. Baseline CORT was similar between strains and unaffected by perinatal food treatments. It was negatively related to body size and body condition. Conversely, the CORT stress response was not markedly affected by physiological condition. It was stronger in wild than in domesticated birds and it increased with age. Birds subjected to prenatal unpredictable food supply exhibited an accelerated development of the CORT stress response which could reflect an adaptive maternal effect. We conclude that the vital role of baseline CORT may allow little adaptive scope since changes can quickly become detrimental. In contrast, the CORT stress response may show considerable adaptive potential which might ultimately support homeostasis in a changing environment.

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1. Introduction

Glucocorticoid (GC) hormones, secreted by the hypothalamic–pituitary–adrenal (HPA) axis, are ubiquitous and crucial in vertebrate life (Sapolsky et al., 2000). GCs orchestrate many physiological processes, including gene expression (Le et al., 2005), energy mobilization (Bonier et al., 2011), reproduction (Schmid et al., 2013), and they also affect behaviour (Coppens et al., 2010). The physiological role of GCs is quite distinct depending on whether they circulate at low baseline or at high acute stress induced levels. GC hormones at low baseline levels exhibit pronounced diurnal patterns and bind to mineralocorticoid receptors (Lattin et al., 2012). They are involved in maintaining physiological homeostasis through allostatic change in everyday life (Bonier et al., 2009; Romero, 2004). In contrast, GC hormone levels rise

drastically within minutes in response to external stressors and bind mainly to glucocorticoid receptors. The GC stress response adjusts physiology and behaviour to the demanding requirements of a stressful event and consequently helps to regain homeostasis after the stressor has been overcome (Sapolsky et al., 2000; Wingfield et al., 1998).

The distinct patterns and physiological role of GCs at baseline and stress response level have been well described in many species, but their fitness consequences and adaptive value for wild animals is less clear (Bonier et al., 2009; Breuner et al., 2008). Thereby, important questions are whether GC excretion is flexible and what environmental factors can affect baseline and stress response during development. Flexibility of the HPA axis could be adaptive in that it integrates environmental cues and thereby helps the individuals to efficiently cope with threads posed by a changing environment. It has been shown repeatedly that at least the GC stress response is, to some degree, under genetic control (Almasi et al., 2010; Odeh et al., 2003). However, the GC stress response is in competition for resources with other physiological processes and it implies costs and benefits which need to be

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balanced (Costantini et al., 2011; Homberger et al., 2013; Wingfield and Sapolsky, 2003). To adequately balance benefits and costs, the GC stress response is modulated by various intrinsic and extrinsic factors e.g. body energy stores (Schultner et al., 2013) or reproductive state (Schmid et al., 2013) and several mechanisms exist that could eventually shape an animal's GC stress response on different time scales. Apart from genetic adaptation, the GC stress response can be affected in the short term by maternal effects (Henriksen et al., 2011), and postnatal early-life conditions can induce transient or permanent alterations of the GC stress response (Lynn et al., 2010; see Macri and Würbel, 2006 for a review of the maternal mediation hypothesis).

In this study we investigated the relative contribution of prenatal and postnatal factors on the developmental trajectories of baseline and stress induced corticosterone (CORT) levels in a wild fowl species, the grey partridge *Perdix perdix*. CORT is the primary GC of birds. We worked with two strains that varied in the duration they were kept and bred in captivity (thereafter called wild and domesticated strain). Parental pairs of both strains and their offspring were subjected to periods of predictable or unpredictable food supply. Unpredictable or insufficient food supply is a potent environmental perturbation which occurs frequently in the wild and could provoke physiological adaptations manifested in GCs levels (Bauer et al., 2011). Throughout the postnatal development, we repeatedly measured levels of baseline and stress induced CORT levels and analysed whether genetic (strain and family origin), prenatal (food unpredictability, common prenatal environment) and postnatal (food unpredictability, social group, individual experience) factors can affect developmental trajectories of baseline and stress induced CORT levels.

We expected that wild strain birds exhibit a strong CORT stress response since this might help them to cope with the high predation risk or facing environmental challenges (i.e. unpredictable weather conditions) in their natural habitats. Conversely, in captivity an animal faces many intense but non-fatal stressors (e.g. handling, human proximity) and a high CORT stress response could be a disadvantage (e.g. through reducing reproduction) and thus selected against (Carrete et al., 2012).

In birds, hormones deposited by the mother into the egg, can affect the offspring's physiology, including the HPA axis (Henriksen et al., 2011; Sockman and Schwabl, 2000). We expected that unpredictable food supply encountered by the mother during oviposition would alter the development of the offsprings' CORT stress response which could be an adaptation to an unpredictable postnatal environment. Postnatal insufficient or unpredictable food supply has been shown to affect baseline and stress response CORT levels (Kitaysky et al., 2001; Reneerkens et al., 2002). We hypothesized that postnatal unpredictable food supply could induce high baseline and stress response CORT levels which could facilitate feeding behaviour after a perturbation has been overcome and when food is available (Lohmus et al., 2006; Wingfield et al., 1997). However, a strong CORT stress response in stressful captive conditions could cause chronic stress manifested in increased baseline CORT (Kitaysky et al., 2001).

Despite developmental and genetic constraints, a high flexibility of CORT profiles has repeatedly been found (Williams, 2008). This flexibility might allow individuals to adopt their own stress coping strategies in accordance with their past experience (Wingfield and Sapolsky, 2003) or in regard of their social group (Creel et al., 2013). Hence, we tested whether full siblings resembled each other in terms of baseline and stress response CORT which could hint at a heritable genetic regulation. We also investigated whether CORT is repeatable within individuals or within members of the same social group.

2. Materials and methods

2.1. Origin of birds

The grey partridge is a ground-dwelling game species with a wide distribution across Europe and western Asia. It is seasonally monogamous and typically has one big clutch per year which can exceed 20 eggs (Potts, 2012). The species is highly sociable. For example, after hatching, families form strong bonds, i.e. coveys, which are maintained throughout the breeding season and the subsequent winter and only disintegrate in the subsequent spring (Potts, 2012). Coveys show pronounced flocking behaviours, i.e. covey members stay close together and activities such as feeding and vigilance are highly coordinate within coveys which can affect survival of group members (Watson et al., 2007).

In 2009 and 2010, we collaborated with a breeder in the UK (Perdix Wildlife Solutions, Warwickshire, UK) who bred partridges of two strains. For the first strain, male and female grey partridges were captured from a sustainable wild population on a large wild game shooting estate in eastern England. Female offspring from these wild pairs were mated with males captured in the wild the consecutive spring. Offspring of this semi-wild strain were subjected to the prenatal treatment at the breeder's place (see below) and produced part of the eggs for our study (wild strain birds). Birds from the second strain were kept and bred in captivity for over 30 generations; no new wild-caught birds were added to this captive population (domesticated strain). We assumed that the captive population of wild birds genetically closely resembles wild-living partridges, while in the domesticated strain adaptations to captivity might have occurred (Homberger et al., 2013). A pilot study found significant differences in polymorphic satellite markers between the two strains, but no signs of inbreeding in either strain (B. Homberger, unpublished data). Parental pairs of these two strains were kept together at the breeders' site in the UK and produced eggs for our study under the experimental conditions described below.

2.2. Experimental procedure

During the breeding season, pairs of wild and domesticated partridges were held in outdoor aviaries in England (3 × 3 × 1.5 m) and randomly assigned to two feeding regimes. Pairs in the first feeding regime had 24 h access to food and water, and thus access to food and water was fully predictable (prenatal predictable food supply). In the second feeding regime, food was removed during four hours a day at randomly differing times between 8 am and 8 pm (thus unpredictable) in accordance with the UK regular feeding schemes (prenatal unpredictable food supply). Eggs were collected daily from all aviaries and transported to Switzerland by airplane at weekly intervals. Artificial incubation and chick rearing took place in our facilities in Switzerland. In 2009 we had a total of 22 parental pairs (11 of each strain) and subjected 5 pairs per strain to the predictable and 6 pairs per strain to the unpredictable feeding regime. In 2010, from a total of 50 parental pairs (25 of each strain), 12 pairs per strain were subjected to the predictable and 13 pairs to the unpredictable feeding regime. On average the parental pairs laid 42.3 (± 3.2 CI) eggs and the number of eggs did not differ between the four strain by prenatal treatment combination groups (Pearson's Chi-squared test: $\chi^2 = 1.09$, d.f. = 1, $P = 0.3$). The number of birds hatched and raised in each treatment group is indicated in Fig. 1.

After hatching, chicks were randomly assigned to indoor aviaries (200 × 80 × 80 cm) with approximately 30 birds per hatching date and aviary. Indoor aviary groups consisted of an equal number of birds (i.e. 7 or 8) per strain × prenatal treatment

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