



Small increases in corticosterone before the breeding season increase parental investment but not fitness in a wild passerine bird

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ABSTRACT

Correlative evidence from field studies has suggested that baseline concentrations of corticosterone, the main avian glucocorticoid hormone, affect reproductive strategies in vertebrate species. Such a role is conceivable in light of corticosterone's function as a metabolic hormone in regulating glucose and fat metabolism. From such correlational studies, however, the question has remained open whether glucocorticoid concentrations change in advance of reproductive activities or whether corticosterone concentrations vary passively as a consequence of the individual's reproductive investment and workload. To test such causal relationships, we manipulated corticosterone concentrations prior to the breeding season in adult great tits (*Parus major*) and quantified reproductive investment and success. Two weeks before egg-laying, we administered subcutaneous silastic implants filled with corticosterone that elevated circulating levels within the baseline range for approximately 30 days to adult males and females. Corticosterone manipulation did not affect lay date or yearly offspring production. However, reproductive behaviors were affected by corticosterone treatment: males fed their mates more often during incubation, and females increased incubation of eggs and brooding of nestlings compared to control individuals. Other behaviors during the nestling stage, when the implants were no longer effective, did not differ between the two treatment groups. Our findings do not support the view that baseline corticosterone concentrations, at least at the time of year when we administered implants, change reproductive strategies per se. The current data suggest that baseline corticosterone levels represent internal signals that causally mediate reproductive effort in individuals of a wild bird species. By increasing reproductive investment, baseline corticosterone concentrations may have functions during the breeding season that diverge from the suppressive effects of stress-induced concentrations.

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Introduction

Life history strategies center on the allocation of limited resources to various fitness-relevant traits. Reproduction is a demanding period in the life of organisms, and even individuals from the same population can display large differences in reproductive strategies according to their internal state (John-Alder et al., 2009), individual quality (Altmann et al., 2010), and the ecological circumstances in which they live (Lack, 1968). In recent years, integrative biologists have become intrigued by the possibility to explain individual variation in reproductive strategies from a mechanistic angle, in particular by examining the role of hormonal signals (Williams, 2008; Wingfield et al., 2008).

Corticosterone (the main glucocorticoid in reptiles, amphibians, birds, and some mammals) has been receiving considerable attention as a possible mediator of reproductive decisions in vertebrate species (Angelier and Chastel, 2009; Bonier et al., 2011; Harris et al., 2011;

John-Alder et al., 2009; Love et al., 2004; Moore and Jessop, 2003; Ouyang et al., 2011b). Corticosterone allows animals to cope with predictable changes in their environments (such as the observed elevated concentrations during energetically demanding processes; Piersma et al., 2000; Romero, 2002) and unpredictable events (such as responses to inclement weather conditions; Wingfield et al., 1983). At baseline levels, it acts as a metabolic hormone by regulating glucose and fat metabolism (Harvey et al., 1984; Lea et al., 1992). When the individual experiences an acute and unpredictable noxious stimulus, baseline corticosterone levels rise within the first 3 min, reaching stress-induced concentrations after ~30 min in many species (Wingfield et al., 1982). High stress-induced corticosterone concentrations typically shut down non-essential processes to promote survival functions (Wingfield and Sapolsky, 2003). Given these functions of corticosterone, this hormone has become an obvious candidate for research on the mechanisms that underlie individual variation in reproductive investment.

Indeed, individual variation in both baseline and stress-induced concentrations has been associated with variation in parental effort in a wide range of species (Adkins-Regan, 2008; Bonier et al., 2009b; Comendant et al., 2003; Harris et al., 2011; Lendvai et al., 2007; Love et al., 2004;

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Ouyang et al., 2011b; Patterson et al., 2011). However, these and other studies have indicated that the functions of corticosterone differ at high and low circulating concentrations (e.g., Landys et al., 2006; Romero, 2004): during the reproductive period, low circulating corticosterone concentrations regulate the degree of reproductive investment while high concentrations appear to mediate major decisions, such as whether to continue investing in a brood or rather into processes that promote an individual's survival to the next breeding attempt (Bonier et al., 2009a; Ouyang et al., 2012; Wingfield and Sapolsky, 2003). This view is corroborated by correlative studies that have shown a positive relationship between baseline corticosterone concentrations and parental behavior, suggesting that higher baseline concentrations are necessary for the increased energy turnover during this phase, which in turn predicts high nestling quality and reproductive success (Bonier et al., 2009b, 2011). Experimental elevations of baseline concentrations in female birds during the breeding season also cause increases in parental effort (Crossin et al., 2012), and experimental increases in parental effort cause increases in baseline concentrations (Bonier et al., 2011). However, results from another study manipulating baseline levels were equivocal due to the limited efficacy of the manipulation (Patterson et al., 2011). Conversely, natural or experimentally induced increases in stress-induced corticosterone concentrations have been linked to decreased reproductive investment and even brood abandonment (Angelier et al., 2007; Ouyang et al., 2012; Silverin, 1986; Spée et al., 2011).

Therefore, while the causal role of high concentrations of corticosterone in brood abandonment decisions has been tested experimentally, the causal relationship of low corticosterone concentrations and reproductive investment has remained unclear (Crossin et al., 2012; Patterson et al., 2011). This is in part due to the difficulty of experimentally manipulating corticosterone levels within the baseline range to test for the effects of baseline corticosterone concentrations on reproductive strategies, behavior, and fitness. The absolute concentrations of circulating corticosterone that are reached after administration of a corticosterone-filled implant are critical because corticosterone has different actions depending on whether it binds to the mineralocorticoid or the glucocorticoid receptor (e.g., Lattin et al., 2012; Romero, 2004; Sapolsky et al., 2000). Furthermore, experimental studies have so far also focused on the relationship between corticosterone and reproduction during the parental phase, while baseline corticosterone might influence reproductive investment also before breeding begins (Ouyang et al., 2011b).

In our study population of great tits (*Parus major*), high baseline corticosterone concentrations prior to the breeding season in both sexes predict high parental effort and high reproductive success later during the breeding season (Ouyang et al., submitted for publication). In the current study, we therefore aimed at testing the hypothesis that higher baseline corticosterone concentrations increase reproductive investment by experimentally elevating corticosterone levels within the baseline range for three weeks in adult male and female great tits before egg-laying and observing reproductive behaviors and fitness consequences later during the breeding season. We predicted that individuals implanted with corticosterone would advance lay date, increase parental feeding rates, and — as a result of increased parental effort — would have higher fledgling numbers than control-treated individuals.

Methods

This study was performed in spring of 2011 in an established nest box population of great tits in the mixed forests surrounding Möggingen, Germany (47°N, 8°E; Ouyang et al., 2012). We first initiated a verification study to determine which kind of implant would produce the desired elevation of corticosterone within the baseline range of our study population. Therefore, in early March 2011, we caught 16 males and brought them into outdoor aviaries. All males ($n = 4$ for each treatment group) were given 7 mm long silastic implants (Dow Corning, inner diameter: 1.5 mm) which were either a) left empty; b) filled with crystalline corticosterone with one end sealed and the other end left open; c) filled with corticosterone and sealed at both ends but had punctured holes in diameter of either c) 0.8 mm; or d) 0.3 mm (Table 1). Implants were administered subcutaneously on the side flank, without the use of anesthesia to minimize handling time and avoid complications from and reactions to the anesthetic. After implantation, the <1 mm skin opening was sealed with veterinary skin glue. We found that the filled implant sealed at one end and with the 0.3 mm hole had the desired effect of a slight (~2 fold) elevation of baseline corticosterone concentrations for ~35 days. Birds from the four treatment groups did not differ in baseline corticosterone concentrations on day 1, right before implantation (Kruskal–Wallis: $df = 3$, $\chi^2 = 1.52$, $p = 0.68$). By day 3, there was a significant difference among treatment groups in baseline corticosterone levels (Kruskal–Wallis: $df = 3$, $\chi^2 = 13.2$, $p = 0.004$), with the open-end and 0.8 mm hole implants resulting in corticosterone concentrations that were in the stress-induced range for great tits (Ouyang et al., 2011a). By contrast, implants with a 0.3 mm hole led to corticosterone levels within the baseline range of our population of great tits (Table 1; range: 0.5–25 ng/mL; Ouyang et al., 2011a). By day 30, baseline corticosterone levels had remained elevated within the baseline range in the 0.3 mm group (Kruskal–Wallis: $df = 3$, $\chi^2 = 7.8$, $p = 0.05$), while titers in the other two treatment groups had returned to pre-implant levels indicating that they had ceased releasing hormone. By day 40 after implantation, individuals carrying the implant with the 0.3 mm hole had corticosterone levels that now were indistinguishable from those before implantation (paired sample t -test: $t = 0.83$, $df = 3$, $p > 0.7$). Body mass of individuals from the 0.3 mm hole treatment and from the control group did not differ on day 3 ($F_{1,6} = 1.0$, $p = 0.36$) nor at any other time points (days 30 and 40) post treatment (p 's > 0.20).

For the field study, 2–3 weeks pre-egg laying (from March 18th to March 25th), we caught adult great tits in mist nets and implanted 12 male and 11 female great tits with corticosterone implants sealed at both ends with a punctured hole of 0.3 mm in diameter, and 12 males and 12 females with empty implants as controls. To avoid the confounding effects of age on reproductive success and hypothalamic–pituitary–adrenal (HPA) axis status, we only used first-year adults in this study. Implants were administered as in the validation study (see above) and birds were then immediately released again at the site of capture.

In May, when their young were 8–9 days old, all implanted individuals were recaptured with manually triggered spring traps at their nest box. A blood sample was taken within 3 min of capture

Table 1

Baseline corticosterone plasma concentrations (ng/mL) produced by different implant types in male great tits. $N = 4$ for each implant type, data are given as mean \pm 1 standard error.

Implant type	Day 1 (before implantation)	Day 3 (after implantation)	Day 30	Day 40
Control implant	10.6 \pm 3.3	8.6 \pm 1.2	8.5 \pm 3.6	
Open on one end	10.9 \pm 2.3	151.6 \pm 28.4	10.5 \pm 2.5	
0.8 mm hole	10.3 \pm 1.8	58.2 \pm 6.0	9.3 \pm 3.6	
0.3 mm hole	11.8 \pm 1.9	22.3 \pm 1.2	19.7 \pm 2.0	10.8 \pm 1.7
Date relative to life history stage of the free-living population	Implant day	Days 10–18: date of first egg	Days 23–30: incubation ends Days 24–31: hatch date	Days 33–40: young are day 8

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