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Corticosterone and brood abandonment in a passerine bird

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Hormones regulate decision-making strategies, in particular by translating an individual's physiological state into decisions on major behavioural and life-history processes, such as reproduction. Corticosterone, a glucocorticoid hormone, has been gaining attention as a mediator of reproductive effort, and experimentally elevated corticosterone concentrations have been shown to disrupt reproduction in avian species. Here, we tested whether individual variation in corticosterone concentrations is related to the decision for brood abandonment in free-living great tits, *Parus major*. Because of harsh environmental conditions, many adults abandoned their first broods in 2010, enabling us to ask which physiological, environmental and individual characteristics increased the probability of nest desertion by both males and females. The best predictors of nest desertion were high stress-induced corticosterone levels in males and low average nestling mass. Furthermore, high stress-induced corticosterone levels in 2010 appeared to represent plastic responses to environmental conditions and reproductive investment: individual males that abandoned their nests in 2010 had higher stress-induced corticosterone concentrations and produced nestlings with lower average mass than in 2009, when nesting successfully. Females that abandoned their nests in 2010 had higher baseline corticosterone concentrations than in 2009, when nesting successfully. Also, males that renested after abandonment in 2010 had lower stress-induced corticosterone concentrations and nestlings with higher mass. Finally, pairs that abandoned but renested later in 2010 had similar fledgling success at the end of the season as those that did not abandon. These results indicate that an individual's reproductive decision is the result of a plastic modulation of the corticosterone stress response that influences reproductive decisions according to environmental conditions.
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A prominent role of hormones is to mediate transitions between life-history stages and regulate behavioural decisions, such as the extent of investment into reproductive effort (Adkins-Regan 2005). However, how animals are able to integrate internal and external conditions to modulate their behaviour and the time course at which such physiological responses occur remain to be clarified. Evidence is mounting that glucocorticoids are mediators of physiological and behavioural responses to challenging events, as well as regulators of the trade-off between current and future reproduction (Sapolsky et al. 2000; Wingfield & Sapolsky 2003; Breuner et al. 2008; Angelier & Chastel 2009; Bonier et al. 2009; Hau et al. 2010; Ouyang et al. 2011a).

At baseline concentrations, glucocorticoids (in birds: corticosterone) serve to maintain energy balance (Harvey et al. 1984), peaking with increased activity and energy demands (Romero 2002; Lormée et al. 2003). Corticosterone concentrations further rise after the animal experiences a stressor, typically reaching maximal concentrations within 30–60 min following a standardized capture and restraint protocol designed to simulate a stressful event (Wingfield et al. 1982; Canoine et al. 2002). Experimentally elevated concentrations that result in an elevation of corticosterone to stress-induced concentrations for several days can inhibit reproduction and induce nest abandonment (Silverin 1986; Wingfield & Silverin 1986; Wingfield & Sapolsky 2003; Spée et al. 2011). Given the dramatic negative effects of high corticosterone levels, it has been suggested that the stress-induced rise in corticosterone concentrations should be down-regulated in individuals for which the value of current reproduction is high to avoid jeopardizing their current reproductive attempt (Wingfield et al. 1992, 1995; Astheimer et al. 1995; Lendvai et al. 2007). Likewise, this endocrine stress response should also be down-regulated in individuals for which the probability of renesting is low (Holberton & Wingfield 2003; Heidinger et al. 2006). Conversely, individuals should up-regulate their stress response if the value of current reproduction is low. However, while lower stress-induced corticosterone concentrations have been frequently found in situations where brood value is high (Lendvai et al. 2007; Bokony et al. 2009),

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the opposite regulation has so far been rarely documented (Groscolas et al. 2008).

Brood abandonment represents a major reproductive decision, especially in species that usually breed once in a season (Székely 1996; Hõrak et al. 1999; Vélez et al. 2002; Pogány et al. 2008). In avian species, the probability of nest desertion depends on individual body condition (Groscolas et al. 2008), environmental variability (Carlisle 1982; Breuner 2011), age (Charlesworth & Leon 1976; Heidinger et al. 2010), sex (O'Reilly & Wingfield 2001) and nestling condition (Trivers 1972). Experimental studies show that large increases in corticosterone concentrations during the breeding season result in decreased parental effort and subsequent nest desertion (Silverin 1986; Spée et al. 2011). However, experimental elevations of corticosterone mimic the natural situation only to a limited extent, and there is therefore a need for studies to exploit individual variation in hormone levels to understand whether corticosterone is indeed the signal involved in reproductive decisions under natural conditions (Williams 2008; Clutton-Brock & Sheldon 2010).

In the only study that we are aware of investigating the effect of corticosterone on brood desertion under natural conditions, Love et al. (2004) found that female free-living European starlings, *Sturnus vulgaris*, with higher free baseline corticosterone levels were more likely to abandon reproduction. Love et al.'s study suggested that baseline, rather than stress-induced, corticosterone concentrations are related to reproductive decisions, in contrast with the results of the above-noted studies. However, in their study, Love et al. (2004) focused on females only, and hormonal mechanisms could differ between the sexes, both of which are making decisions about abandonment (Pogány et al. 2008). Hence, more research on both members of a pair, with a focus on individual variation in stress physiology and decision making, is needed to resolve this question. Also, it is important to further our understanding of the time course as well as the exact nature of the relationship between corticosterone and brood desertion decisions (i.e. whether individual quality is reflected in corticosterone concentrations, or whether corticosterone is regulated independently of individual quality to mediate reproductive decisions depending on environmental conditions).

In the current study, we evaluated potential variables involved in decision-making about brood abandonment by both sexes to present a comprehensive picture of the processes that guide reproductive decisions. We took advantage of data from a free-living songbird population collected over 2 years, which differed dramatically in environmental conditions. We expected that baseline corticosterone levels would be correlated with environmental conditions, with lower ambient temperatures increasing parental energy expenditure and thus baseline concentrations. Conversely, we predicted that stress-induced corticosterone concentrations would be indicative of reproductive decisions, in which higher concentrations would increase the likelihood of nest desertion. Moreover, we expected that younger parents with lower body mass and fewer offspring of lower average mass would be more likely to abandon their nests (Hõrak et al. 1999). Lastly, as with our predictions above for different individuals, we expected corticosterone concentrations to vary in similar ways within individuals (i.e. when comparing breeding attempts of an individual within and between years).

In our population of free-living great tits, *Parus major*, from southern Germany, the percentage of second broods is usually very low (around 4%); nest predation in this nestbox-occupying species is also very low (Sanz 1998). Hence, the first reproductive attempt in a given season is most likely the only breeding attempt for an individual in that year. We performed a capture–restraint protocol (Wingfield et al. 1982) for all adults during the parental stage of the first brood in two subsequent years to assess their endocrine responses to a stressor in a standardized way while closely monitoring their reproductive investment, especially nest desertion. In 2009, a year with good environmental conditions, we recorded few nest abandonments in our study population (2% for $N = 52$ nests). By contrast, 2010 was an unusual year because of high rainfall, low ambient temperatures and low food availability (see Results), resulting in 37% nest abandonment during the late nestling phase ($N = 71$ nests in total). Thus, the inclement weather provided an ideal natural experiment to examine the role of corticosterone as a mediator of reproductive decisions by enabling us to monitor when and whether individuals ceased reproduction based on environmental conditions, hormonal profile, body mass and brood value.

METHODS

Study Site and Standard Protocols

This study was carried out between March 2009 and July 2010 in Moeggingen, Germany (47°N, 8°E), a 1.5 km^2 stand of mixed forest in which 306 nestboxes were placed in 2007. Nestboxes were checked every week starting in late March and then every day from the date the nest was complete to the start of incubation. Nests were monitored again daily as hatching date approached, so that the exact date of the first egg to hatch could be recorded (noted as day 1). Nestlings were then monitored every 5 days until fledging, and the total number of fledglings was recorded for each nest. Many of the pairs that abandoned their first broods in 2010 renested later in the season, and were then monitored in the same way.

Adult great tits were captured in their nestbox between 0800 and 1200 hours with a manually triggered metal trap that sealed the entrance hole when adults entered to feed their 8- or 9-day-old nestlings. In 2010, there was no effect of time of capture ($N = 149$) on baseline corticosterone (Pearson's correlation: $r = -0.09$, $P = 0.34$), stress-induced corticosterone ($r = -0.03$, $P = 0.72$), ambient temperature ($r = -0.09$, $P = 0.28$; temperatures remained low throughout the morning because of heavy rainfall), or individual body mass ($r = -0.11$, $P = 0.29$). Both the male and female were caught at every monitored nest. We noted the ambient temperature at the time of capture from a temperature logger that was placed on the outside of a nestbox at the field site (Scanning Devices, Inc., Lexington, MA, U.S.A.). Blood samples (80–120 µl) were taken within 3 min (mean ± SD = 1.9 ± 0.9 min, $N = 149$) of capture for later determination of baseline corticosterone concentrations. Birds were then placed in a cloth bag for a standard capture–restraint procedure (Wingfield et al. 1982; Ouyang et al. 2011a). While the adults were held captive (for maximally 35 min; see Ethical note), we weighed all chicks to the nearest 0.1 g (chicks were kept on warming pads until the entire brood had been weighed and were returned to the nest immediately after the weighing process). Another blood sample (50 µl) was taken at 30 min postcapture to assess stress-induced corticosterone concentrations. After completion of the second blood sample, we released the adults after determining their body mass (to the nearest 0.1 g) and tarsus length (to the nearest 0.1 mm). Adult age was scored from plumage (Jenni & Winkler 1994) as a first-year breeder or older, or was inferred from previous banding records. Blood samples were immediately stored on ice and centrifuged (822× *g*, 10 min) within 4 h; the plasma was separated and stored at −80 °C.

After releasing captured adults, we immediately monitored their nestbox from a distant blind to observe when the adults returned to the nest (which usually occurred within 5 min after release if the adults did not abandon the nest). We continued

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