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Evidence for baseline glucocorticoids as mediators of reproductive investment in a wild bird

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ABSTRACT

Determining the mechanisms that mediate investment decisions between current and future reproductive attempts is still a key goal of life-history studies. Since baseline levels of stress hormones (glucocorticoids – GCs) act as predictive and labile regulators of daily energetic balance in vertebrates they remain excellent candidates for mediating investment decisions both within and across reproductive attempts. Using free-living female European starlings (*Sturnus vulgaris*) we experimentally reduced investment in current reproduction (number of offspring raised in the first brood) to examine whether baseline corticosterone (CORT) acted as a hormonal mediator preparing individuals for a predictable increase in future investment (number of offspring raised in the second brood). Although treatment and control birds raised the same total amount of offspring across two broods, the experimental birds increased reproductive investment in second broods to compensate for the reduced investment in the first brood. Data on both mean and intra-individual changes in baseline CORT support the idea that an increase in baseline CORT between the incubation stages in treatment birds strongly predicted this increase in investment. Importantly, we measured the increase in baseline CORT during late incubation prior to the increase in energetic demand associated with increased reproductive investment in offspring, indicating that flexible within-individual changes in baseline GCs can act as a labile mechanism preparing individuals for predictable increases in reproductive investment. As such, our experimental results indicate that elevated baseline GCs can prepare individuals for investment in energetically expensive life-history stages, rather than simply being elevated as a consequence of increased effort or demand. This suggests that short-term preparative increases in baseline GCs benefit individuals by successfully allowing them to maximize fitness under varying environmental conditions.

1. Introduction

Life-history theory predicts that individuals must optimize investment across reproductive attempts to maximize lifetime reproductive success (Stearns ,1992). Empirical studies have confirmed that investment in current reproduction influences both future investment decisions, survival and lifetime reproductive success (Nur, 1984, 1988; Dijkstra et al., 1990; Daan et al., 1996; Love and Williams, 2008a). However, establishing the underlying mechanisms that mediate fine-scale adjustments in investment across breeding attempts has not been forthcoming (Love and Williams, 2008a). Field endocrinologists have long appreciated that acutely elevated stress-induced levels of glucocorticoids (GCs) can influence reproductive decisions such as reproductive abandonment (Wingfield, 2005; Romero et al., 2009). Recently, integrative biologists have begun examining variation in baseline GC levels as relevant candidates for mediating investment decisions (Hennin et al., 2012; Love et al., 2013; Sheriff and Love, 2013) both within and across reproductive attempts given their predictive and labile role as regulators of daily energetic balance in vertebrates (Sapolsky et al., 2000; Remage-Healey and Romero, 2001; Landys et al., 2006). More specifically, baseline GCs (i) follow a highly predictable diel cycle peaking before resources are required (Dallman et al., 1993; Remage-Healey and Romero, 2001), (ii) mediate increases in foraging behavior (Breuner et al., 1999; Kitaysky et al., 2001; Crossin et al. 2012), (iii) peak seasonally during reproduction (Romero, 2002), and (iv) are at their highest during the most

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energetically demanding periods of reproduction (Moore and Jessop, 2003; Love et al., 2004; Rubenstein and Wikelski, 2005; Bonier et al., 2009b).

Recent work on the interaction between baseline GCs and reproduction in free-living systems has primarily focused on determining their relationship to fitness (i.e., the "CORT-Fitness" hypothesis; Bonier et al., 2009a; Angelier et al., 2010; Romero and Wikelski, 2010; Low et al., 2012; Love et al., 2013). Although the "Context-Dependent" hypothesis formalized the concept that an increase in baseline GCs could promote allocation of resources towards reproduction when the value of the current reproductive attempt is high (Bonier et al., 2011), studies to date have all involved experimentally increasing baseline GCs and then measuring responses within the immediate reproductive attempt (e.g., Bonier et al., 2009b, 2011; Crossin et al., 2012; Ouyang et al. 2013). However, researchers have not manipulated investment in current investment, measured changes in future investment and then determined whether the quantitative change in baseline GCs between attempts are in themselves predictive of the relative change in investment. Distinguishing whether elevated baseline GCs are a cause or consequence of increased reproductive investment allows us to determine whether baseline GCs have the potential to play significant roles in mediating variation in life-history traits and fitness (Harshman and Zera, 2007). Moreover, while experimental manipulations of absolute baseline GCs in free-living systems have illustrated that elevated baseline GCs influence investment within a given reproductive stage (Crossin et al., 2012; Ouyang et al., 2013), life-history theory predicts that it is flexibility in the mechanisms (in this case changes in baseline GC levels across multiple reproductive attempts) that will influence an individual's ability to balance investment across current and future reproduction (e.g., Angelier et al., 2007, 2010). To our knowledge, no study has causally tested whether quantitative changes in baseline GCs mediate the optimal management of reproductive decisions across breeding attempts to ultimately maximize fitness.

Using free-living female European starlings (*Sturnus vulgaris*), we causally tested whether intra-individual changes in baseline corticosterone (CORT) mediated reproductive investment across two intra-annual broods. We measured baseline CORT during late incubation of the initial clutch and then experimentally reduced the number of offspring raised in that first brood by 50% (i.e., we reduced investment in current reproduction). We then measured baseline CORT during late-incubation of the second clutch and allowed females to raise the brood normally. Based on optimal investment theory for short-lived species (i.e., Drent and Daan, 1980), we expected that a reduction in current (first-brood) reproductive investment would induce an increase in future (second-brood) reproductive investment designed to maximize intra-annual reproductive output (Stearns ,1992). If baseline GCs can act as mediators of reproductive investment, we predicted that baseline CORT would be elevated from first to second brood incubation as a mediatory mechanism to prepare for the expected increase in brood demand. Moreover, we predicted no treatment differences in local survival to the next year given that increases in baseline GCs should mediate optimal reproductive investment.

2. Materials and methods

2.1. Study site, manipulation and sampling protocol

We carried out fieldwork from April–July 2007 on a population of nest box-breeding European starlings in British Columbia, Canada (49°10′N, 122°50′W), under a Simon Fraser University animal care permit (659-B), following Canadian Council on Animal Care guidelines. Starlings at this site lay 5.88 ± 0.10 eggs/clutch within their first breeding attempt, incubate for 10.2 ± 0.1 days, fledge nestlings in 21 ± 0.4 days following hatching, and produce two viable broods per season (mean ± sem; $n = 162$; Love and Williams, 2008a). The study site consists of 190 nest boxes checked daily to determine clutch initiation, laying sequence, and clutch completion dates. We used only females within the synchronous first peak of egg-laying (the first 6–7 days of laying; Christians et al., 2001). To remove any remaining incubation-related investment effects among individuals, we adjusted all clutches to the same size. To remain conservative, given that some females had laid five-egg clutches, we did not wish to increase incubation investment for any females and as such chose 5 eggs as the equality clutch size.

All females were captured and blood sampled 1–2 days before hatching of their first clutch (i.e., late incubation). Blood was collected in heparinized capillary tubes from the brachial vein within 2 min of the nest hole being covered (86.9 ± 5.37 s – mean ± sem) to measure circulating baseline CORT (samples centrifuged within two hours at 12,000 rpm, and plasma stored at −20 °C). Females were then weighed/measured (body mass: ±0.1 g; wing and tarsus: ±1 mm), banded with metal and color bands, and released. At hatching, we experimentally manipulated the size of first broods to alter current reproductive investment: (i) "control females" ($n = 10$) were given six nestlings (the mean brood size during the peak of laying); (ii) "reduced-brood females" ($n = 8$) were given three nestlings (i.e. half the mean brood size during the peak of laying). Nestlings were randomly exchanged between experimental broods at hatching and were matched by hatching date. All females returned to lay a second clutch and were re-captured and rapidly blood sampled (89.9 ± 5.37 s – mean ± sem) 1–2 days before hatching of their second clutch. Females were then left to rear their desired brood size based on individual decisions in how much to invest in future reproduction. Females were followed through to 2008 to gauge local survival.

2.2. Hormonal and statistical analyses

Baseline corticosterone was determined using a previously validated Enzyme-Linked-Immunosorbent Assay (ELISA-Assay Designs Inc., Michigan USA, catalog #901-097; see Love and Williams, 2008b) with a 4-parameter logistic fit. Samples were run in triplicate across two assay plates at a total well volume of 100 µl with 1:40 dilution and 1.5% steroid displacement buffer. As per kit instructions, plates were first incubated at 26 °C under shaking at 5000 rpm for 2 h and then at 26 °C without shaking for 1 h. The detection limit of the assay was 0.018 ng/well (0.72 ng/ml), with intra- and inter-assay variations of 3.8% and 7.8%, respectively. No relationship between CORT levels and the time after capture indicated true baseline CORT levels had been obtained. General Linear Mixed Models were used to examine inter-individual variation in reproductive investment and baseline CORT and baseline CORT was log-transformed prior to analyses to obtain normality. All analyses were performed using JMP 8.0 (SAS Institute) and mean ± sem are reported.

3. Results

3.1. Treatment effects on change in reproductive investment

There was no difference in initial clutch size for females allocated to experimental treatments ($F_{1,25} = 2.28$, $p = 0.21$; control: 6.09 ± 0.19 eggs; reduced: 5.88 ± 0.23 eggs; controlling for lay date; Fig. 1a). Control females raised more nestlings than experimentally reduced-brood females in their first reproductive attempt ($F_{1,25} = 63.4$, $p < 0.001$; control: 5.10 ± 0.31 nestlings, reduced: 2.87 ± 0.12 nestlings; Fig. 1b). While all females laid a second clutch, there was no treatment difference in clutch size

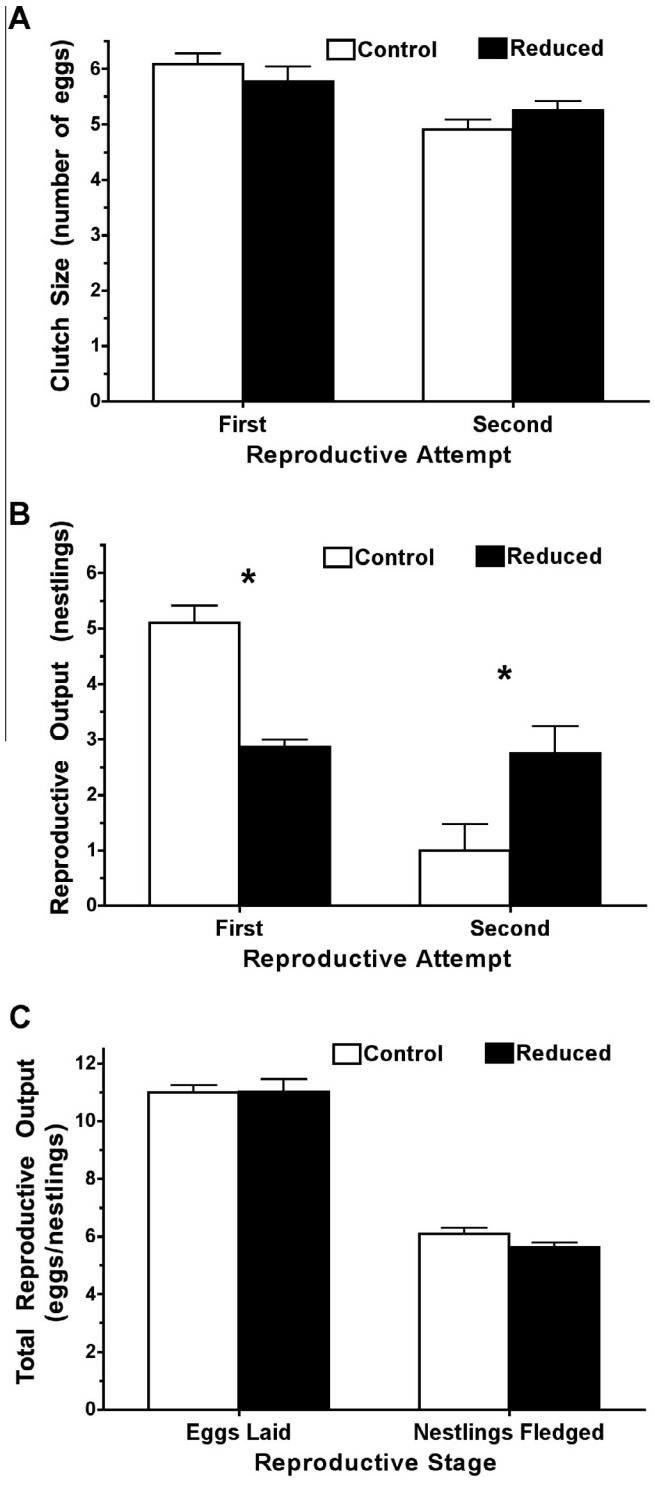

Fig. 1. Treatment effects on current and future reproductive investment decisions and intra-annual reproductive output in female European starlings–clutch size (A), the number of nestlings fledged (B) and total reproductive output (C) for 'control' and 'reduced females' (see Methods for manipulation details).

(T-ratio = −1.41, $p = 0.18$; control: 4.90 ± 0.18 eggs, reduced: 5.25 ± 0.16 eggs; Fig. 1a). However, reduced-brood females invested more heavily in second attempts and fledged significantly more nestlings compared to control females (T-ratio = −2.55, $p = 0.02$; control: 1.00 ± 0.47 nestlings, reduced: 2.75 ± 0.49 nestlings; Fig. 1b). Nevertheless, the total annual reproductive output across both broods did not differ between treatment groups (Clutch size: $F_{1,15} = 0.89$, $p = 0.86$; control: 10.99 ± 0.26 eggs, reduced: 11.03 ± 0.43 eggs; Nestlings: $F_{1,10} = 1.42$, $p = 0.26$; control: 6.10 ± 0.66 nestlings, reduced: 5.62 ± 0.53 nestlings; Fig. 1c). Although body mass significantly decreased across breeding attempts, changes were independent of treatment (GLMM, treatment: $F_{1,15} = 1.99$, $p = 0.18$; brood: $F_{1,14} = 23.31$, $p < 0.0001$; treatment × brood: $F_{1,14} = 1.30$, $p = 0.27$). Finally, the local survival of females to the following year did not differ by treatment (T-ratio = 0.82, $p = 0.71$; return rate-control: 63.3 ± 5.9%, reduced-brood: 66.2 ± 8.9%).

3.2. Mediation of reproductive investment by baseline CORT

Late-incubation baseline CORT measured in the first reproductive attempt did not differ among females assigned to the "control" or "reduced-brood" treatment (T-ratio = 2.12, $p = 0.08$; un-transformed baseline CORT-range: 2.16–67.46 ng/ml; mean: 12.35 ± 2.05 ng/ml). There was a significant treatment × breeding attempt interaction on baseline CORT (GLMM, treatment group: $F_{1,16} = 0.10$, $p = 0.75$, brood: $F_{1,16} = 1.84$, $p = 0.19$, treatment × brood: $F_{1,16} = 9.25$, $p < 0.01$; Fig. 2): baseline CORT levels decreased in control females across attempts (mean change: −39.52%; Fig. 2), but increased across attempts in reduced-brood females (mean change: +34.01%; Fig. 2). Moreover, the increase in baseline CORT measured between late-incubation of the first to the second clutch strongly predicted the subsequent increase in reproductive investment from first to second reproductive attempts (non-linear regression: $r^2 = 0.73$, $p = 0.0004$; Fig. 3). Finally the local survival of females to the following year was not predicted by the inter-attempt change in baseline CORT from the

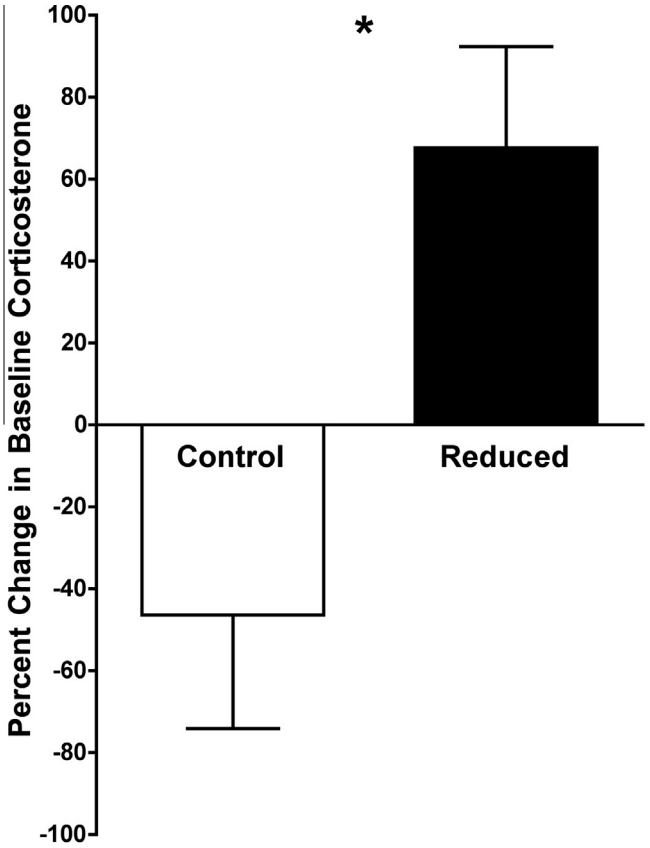

Fig. 2. Treatment-induced changes in baseline corticosterone measured during late incubation of the two within-season reproductive attempts in female European starlings (* denotes a significance of $p < 0.05$).

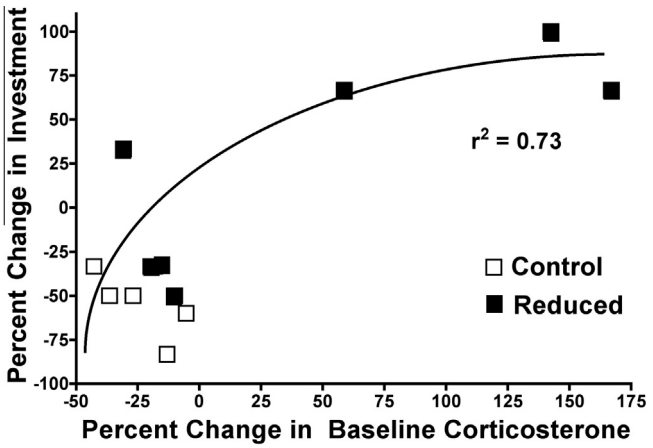

Fig. 3. Change in baseline corticosterone measured during late incubation of the two within-season reproductive attempts mediates the change in reproductive investment in female European starlings.

previous year in either treatment (logistic regression: control: $X^2 = 1.49$, $p = 0.28$; reduced-brood: $X^2 = 1.01$, $p = 0.41$).

4. Discussion

Using optimal investment theory as a basis (Drent and Daan, 1980) we were able to causally test the underlying mechanisms that mediate current versus future reproductive investment trade-offs (Stearns, 1992). Our experimental results confirm that elevated baseline GCs can mediate an increase in future investment and are not simply a consequence of increased effort or demand. Following the imposed reduction in first brood (current) investment, experimental birds increased baseline CORT prior to investment in the second (future) brood, resulting in an increase in investment that enabled individuals to maximize reproductive output over the breeding season (i.e., obtain the same reproductive output as control birds). Importantly, the increase in baseline GCs strongly predicted the relative increase in this future investment. While experimental manipulations of baseline GCs have reported positive investment responses within reproductive attempts (e.g., Bonier et al., 2009a, 2011; Crossin et al., 2012; Ouyang et al., 2013), our results are the first to show that preparative elevation of baseline GCs can enable individuals to successfully manage investment decisions across reproductive attempts. These findings suggest that it is the optimal management of baseline GCs across breeding attempts, and likely across a life span, which enable individuals to maximize lifetime reproductive success (i.e., fitness).

In the current study, five lines of evidence causally support the prediction that an increase in baseline GCs mediated an increase in reproductive investment, rather than higher investment leading to an increase in baseline GCs due to the demand of reproduction. First, although investment in the first brood was manipulated, birds were left to make their own optimal decisions about investment in second broods. As such, this manipulation represented a biologically relevant method of examining how hormonal changes mediated future investment decisions. Second, despite treatment differences in current and future investment decisions, control and experimental birds laid the same number of eggs both within and across the breeding season (i.e., no difference in initial or total investment), and produced the same total number of nestlings by the end of the breeding season. Experimental birds were therefore not forced into allocating more overall and their elevated incubation baseline CORT in second attempts should therefore be attributable to the expected increase in nestling investment, not the result of greater clutch investment. Third, by measuring baseline GCs during late incubation of each attempt we were able to detect whether hormones increased before females invested in their offspring. This design, combined with similar clutch investment by both groups, indicates that the increase in baseline CORT that we observed likely mediated an increase in foraging behavior required to fledge more offspring in the second breeding attempt. Fourth, compared to controls, treatment birds did not lose any more body mass, abandon their offspring to a greater degree, or produce fewer offspring, counter to the argument that the increase in baseline CORT was due to an increase in the "stress" of reproduction (i.e., Bonier et al., 2011). Finally, we did not detect treatment differences in local survival or a relationship between the increase in baseline CORT and local survival, indicating that management of baseline GCs successfully optimized reproductive decisions across attempts.

Recent reviews have failed to detect a concerted, simple relationship between single-point measures of baseline GCs and fitness (e.g., Bonier et al., 2009a). As such, recent theoretical (Dingemanse et al., 2010; Madliger and Love, 2014) and empirical studies (Bonier et al., 2011; Ouyang et al., 2013) have emphasized the need to examine the role that intra-specific variation in baseline GC flexibility (*sensu* intra-specific variation in within-individual changes in baseline GCs across breeding stages or attempts) plays in influencing fitness. Our results linking intra-individual changes in baseline GCs to downstream reproductive decisions may help to explain the lack of a straightforward link between point measures of baseline GCs and fitness. Moreover, our work lends further support to the idea that elevated baseline GCs during energetically demanding life-history stages may not only be the consequence of demand, but may also mediate preparation for this demand. This idea is built upon recent experimental work indicating that elevations of GCs within normal baseline ranges can have a positive effect on foraging and investment in reproduction (Angelier et al., 2007; Crossin et al., 2010; Hennin et al., 2012). These and other recent data highlight the recommendation that evolutionary endocrinologists move beyond the assumption that absolute measures of GCs alone are adequate to predict variation in fitness-related traits (Williams, 2008, 2012; Madliger and Love, 2014). Our results also support recent suggestions that caution against using baseline GCs as measures of individual or population health in species of conservation concern without determining how and why environmental or life-history context influences the link between GCs and fitness (Bonier et al., 2011; Madliger and Love, 2014).

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