

Modulation of the adrenocortical response to acute stress with respect to brood value, reproductive success and survival in the Eurasian hoopoe

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Abstract Reproducing parents face the difficult challenge of trading-off investment in current reproduction against presumed future survival and reproduction. Glucocorticoids are supposed to mediate this trade-off because the adrenocortical response to stress disrupts normal reproductive behaviour in favour of self-maintenance and own survival. According to the brood-value hypothesis, individuals with a low survival probability until the next reproductive season have to invest in current reproduction, a process driven by a down-regulation of their adrenocortical response. If the adrenocortical response to stress effectively mediates the trade-off between current reproduction versus future survival and reproduction, we expect a negative relationship with reproductive success and a positive correlation of the adrenocortical stress response with survival. We studied the relationship between corticosterone secretion in parents and their current brood

value, reproductive success and survival in a short-lived multi-brooded bird, the Eurasian hoopoe *Upupa epops*. The adrenocortical response to acute handling stress was correlated with the brood value within the individual (first and second broods of the year) and between individuals. Birds breeding late in the season mounted a lower total corticosterone response to acute stress than birds breeding earlier, while females showed lower levels than males. We observed a negative relationship between the adrenocortical stress response and rearing success or fledging success in females, as predicted by the brood-value hypothesis. However, we could not evidence a clear link between the adrenocortical stress response and survival. Future research testing the brood-value hypothesis and trade-offs between current reproduction and future survival should also measure free corticosterone and carefully differentiate between cross-sectional (i.e. between-individual) and individual-based experimental studies.

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Introduction

Central to life-history theory is the trade-off between investment in current reproduction versus future survival and reproduction (Stearns 1992). According to this tenet, parents balance the costs and benefits of investment into current reproduction against the probability of their own survival and the presumed costs and benefits of future reproduction (Williams 1966). One hormonal mechanism that is likely to mediate this trade-off is the stress response triggered by the hypothalamo–pituitary–adrenal (HPA) axis (Wingfield et al. 1998; Wingfield and Sapolsky 2003).

Various stressors (e.g. predators, inclement weather, reduced food availability) activate the HPA axis and induce a rise in circulating glucocorticoids (corticosterone in birds). Elevated levels of corticosterone promote energy mobilization, enhance respiration and the cardiovascular system, but inhibit processes that are not immediately vital, such as reproduction and some immune functions (Wingfield et al. 1998; Sapolsky et al. 2000; Perry and Gilmour 1999; Stier et al. 2009). Therefore, if corticosterone surpasses the moderate levels found to potentially favour reproduction (e.g. Bonier et al. 2009; Moore and Jessop 2003), elevated levels of corticosterone may favour survival at the expense of current reproduction and may hence be directly involved in regulating the trade-off between current reproduction versus future survival and reproduction (Ricklefs and Wikelski 2002; Wingfield and Sapolsky 2003).

From life-history theory, it follows that the adrenocortical response to stressors is modified according to the relative value of the current brood, hereafter referred to as the brood-value hypothesis (Heidinger et al. 2006; Lendvai et al. 2007). If the value of the current reproduction is high relative to the value of future reproduction and survival, the stress response should be dampened to ensure that the current reproduction is not compromised (Wingfield and Sapolsky 2003). The brood value is therefore high for species which reproduce only a few times in their lifespan, while it is relatively low for species with extended lifespan and multiple reproduction opportunities.

In birds, the brood-value hypothesis has gained support from many correlative studies at the interspecific and intraspecific level. The adrenocortical stress response has been shown to be attenuated (1) in species with a high relative brood value (a comparison of 64 bird species; Bókony et al. 2009), (2) during the breeding period when most parental care is provided (Wingfield et al. 1995), (3) in the sex that provides more care to offspring (reviewed in Bókony et al. 2009), (4) in long-lived birds at higher age when future opportunities to reproduce decrease (Heidinger et al. 2006; but see Wingfield et al. 1995), and (5) when breeding opportunities are limited (e.g. short-lived passerines in arctic environments; Wingfield et al. 1995). However, there are only a few studies demonstrating that individuals actively modulate their adrenocortical stress response to the experimentally manipulated brood value (Lendvai et al. 2007; Lendvai and Chastel 2008).

To our knowledge, no study has so far investigated whether the adrenocortical stress response during the breeding season is negatively correlated with reproductive success and at the same time positively with survival, both predictions of the brood-value hypothesis. It is well known that experimentally increased corticosterone levels compromise reproduction (Silverin 1985; Wingfield and

Sapolsky 2003; Salvante and Williams 2003; Almasi et al. 2008; Angelier et al. 2009a), especially when glucocorticoids are high for a prolonged time (thus approaching a chronic state). Artificially increased corticosterone levels (silastic implants) reduced apparent survival the following year in black-legged kittiwakes *Rissa tridactyla* (Goutte et al. 2010). However, we found only five studies that explored the relationship between the naturally occurring adrenocortical response to acute stress (as opposed to exogenous corticosterone administration) and survival, and none on the relationship with reproductive success (reviewed in Breuner et al. 2008; Brown et al. 2005; MacDougall-Shackleton et al. 2009; Angelier et al. 2009b). Three of these studies concerned animals outside the reproductive season or nestlings. They found either a negative (Galapagos marine iguana *Amblyrhynchus cristatus*, white stork *Ciconia ciconia* nestlings; Romero and Wikelski 2001; Blas et al. 2007) or a positive or no relationship (American redstarts *Setophaga ruticilla* in their tropical non-breeding area in suboptimal or optimal habitats, respectively; Angelier et al. 2009b) between handling-stress-induced corticosterone levels and survival. One of the two studies carried out with parents during the breeding season found a lower handling-stress-induced response in song sparrows *Melospiza melodia* returning to the same breeding grounds the next year, compared to non-returning conspecifics (MacDougall-Shackleton et al. 2009), while the other could only evidence a weak curvilinear effect in cliff swallows *Petrochelidon pyrrhonota* (Brown et al. 2005). Hence, the expectation that a high natural adrenocortical stress response favours survival is supported by only one study, but disagrees with at least three studies, and we did not find any study looking at the relationship with reproductive success.

In this correlative field study, we tested several predictions of the brood-value hypothesis in a short-lived multi-brooded bird species, the Eurasian hoopoe *Upupa epops*. First, we tested whether the adrenocortical stress response varies with the relative brood value, namely (1) between the first and the second brood within the same breeding season, and (2) between the sexes. We expected to see a lower stress response in broods with a higher relative brood value. The relative brood value is higher when future reproductive opportunities are fewer (all other things being equal; Bókony et al. 2009) and this is the case in second broods and/or in late broods compared to first broods. Late in the season, there is no chance to rebreed during the same breeding season and little chance to breed in a next year, because apparent adult survival was found to be only 38 % in the study population (Schaub et al. 2012). Regarding sex-specific adrenocortical stress response, predictions are difficult. The female invests in egg production, incubation and brooding of young chicks when being fed by the male,

whereas the male makes most of the reproductive effort in terms of food provisioning during all breeding stages (Arlettaz et al. 2010a).

Second, we looked at correlations between adrenocortical stress response and both the current reproductive success and apparent adult survival (i.e. the return rate to the study area the following year). Under the brood-value hypothesis, we expected a negative correlation of the adrenocortical stress response with reproductive success. Individuals with a down-regulated stress response compromise their parental investment less through high corticosterone levels. Conversely, we expected a positive correlation with survival.

Materials and methods

Study site and study species

The study was carried out in a hoopoe population of about 130 broods in the upper Rhone valley, Valais, Switzerland (46°11'N, 7°18'E, about 62 km², 1.9 × 43 km) in 2007 and 2008. For the calculation of return rates, individuals recaptured in 2009 were also used. Almost the entire population breeds in ca. 700 nest boxes provided in agricultural buildings and sheds (Arlettaz et al. 2010a).

The Eurasian hoopoe is a short-lived migratory bird. During the 5 months in the breeding area, hoopoes attempt one or two broods, exceptionally three (Arlettaz et al. 2010a). The female incubates alone and broods the chicks during 8–10 days after the first egg hatches (asynchronous hatching; Martín-Vivaldi et al. 1999), while food for the nestlings and the female is provided by the male. Thereafter, both male and female provision the brood, as long as the female is not monopolized by the incubation of a new clutch (Arlettaz et al. 2010b). The chicks fledge at the age of 23–25 days.

In the study years, 35 % of the birds ($n = 241$) attempted a second brood with the same or another partner, whereas only 3 birds engaged in a third brood. In order to determine whether an individual attempted one or two broods within a year, we tried to catch all parents at each brood. Individuals that were captured at two different broods within a year clearly attempted a first (breeding attempt category 1) and a second brood (category 2). Individuals captured only once in a year were assigned to two additional categories, one for early (category 1a) and one for late (category 1b) breeders, with the separation date between early and late broods fixed according to the trough between the two modes of the frequency distribution of hatching dates for categories 1 and 2 (7 June in 2007 and 5 June in 2008). Because we caught the parents at 82 % of the broods, and because there were hardly any broods in the

study area outside our nest boxes, it is very likely that birds caught only once were actually attempting only one brood in the study year.

Clutch size and brood size at fledging respectively were 8.12 ± 0.12 (SE) eggs and 5.12 ± 0.28 fledglings for breeding attempt category 1; 8.22 ± 0.13 eggs and 4.96 ± 0.24 fledglings for breeding attempt category 1a; 6.80 ± 0.12 eggs and 3.48 ± 0.16 fledglings for breeding attempt category 2; 7.06 ± 0.20 eggs and 3.56 ± 0.24 fledglings for breeding attempt category 1b.

Brood value and reproductive success

The relative brood value compares the value of the current brood with the value of all future reproduction of the individual. Following Bókony et al. (2009), the value of the current brood relative to the value of all future broods can be calculated as the number of chicks (or eggs) of the current brood divided by the number of chicks (or eggs) to be expected in all following broods. The relative brood value, therefore, is a within-individual measure and is independent of brood size if brood size is constant within the individual. This is in contrast to measures of reproductive output (as, e.g., a measure of a fitness component) which compare the number of offspring between individuals, rather than within the individual, and in which the number of offspring is a key component.

In the case of the hoopoe, with one or two annual broods, the relative brood value of the first brood is lower when there is a second brood in the same year than when there is only a single brood, assuming that survival and reproduction during subsequent years does not strongly depend on the number of broods during the current year. Apparent survival increases with increasing number of fledglings produced in a breeding season (Bötsch et al. 2012). Since a large number of fledglings can only be produced when two broods are raised in a breeding season, the positive correlation between apparent survival and fledgling production would attribute an even lower value to the first broods of individuals with two annual broods, because they can not only have a second brood but they also have a higher chance to breed the next year. Therefore, our prediction is that the brood value of the current brood is low for birds breeding early in the season, which have the chance to have a second brood during the same year. Conversely, the brood value is high for birds which breed late in the season; their next chance to reproduce is only during the next year, which they live to see with a survival rate of only 38 %.

We used two measures of reproductive success: (1) the total number of chicks close to fledging as an overall measure of reproductive output and (2) the rearing success, i.e. the proportion of eggs that gave rise to fledglings. The

reasons for using rearing success were twofold. First, by using rearing success, we could directly assess the effect of corticosterone on parental rearing investment, independently of the number of eggs laid. The number of eggs laid varied from 3 to 11 (mean = 7.65 ± 1.36 SD) and therefore strongly influenced the number of chicks at fledging (generalized linear model with brood size at fledging as dependent variable and clutch size as explanatory variable using Poisson distribution and single term deletion to test significance: $p_{\text{Chi}} < 0.0001$). The number of eggs laid is probably under the influence of environmental factors operating well before the chick rearing period. Second, we assessed the adrenocortical stress response during the chick rearing period, and not during egg laying. Rearing success predominantly depends on incubation and food provisioning, because nest predation is nearly nonexistent in hoopoes breeding in nest boxes (own observations). Rearing success in our population is probably an excellent indicator of parental investment (Arlettaz et al. 2010b).

Capture, blood sampling and body condition

The males were caught with a spring trap at the nest box entrance or with a mist net put in front of the nest box when nestlings were 2–26 days old. The females were either caught by hand in the nest box while brooding (nestling age 1–10 days) or captured like the males while feeding the chicks (nestling age up to 19 days). Eighty-five out of 241 adults were blood-sampled at two different broods within the same year.

At each capture-blood-sampling occasion, two blood samples were taken by puncturing the alar vein, one on each wing. The first blood sample was taken as soon as possible after capture (<3 min) to represent baseline levels of corticosterone (Romero and Reed 2005). After weighing and measuring the bird, a second blood sample was taken within 20–30 min (1,200–1,880 s) after capture (75 % between 20 and 24 min; mean: $1,372 \text{ s} \pm 133 \text{ SD}$, $n = 326$). These samples provided values induced by capture, handling and restraint stress (handling-induced samples; Wingfield et al. 1992; Wingfield 1994).

Blood was collected in Na-heparinized microcapillary tubes. Within about 5 min after taking the second sample, the blood was centrifuged for 5 min, and the plasma stored in liquid nitrogen in the field, then conserved in a deep freeze at $-20 \text{ }^\circ\text{C}$ until analysis.

The sex of the adults was determined by inspection of the uropygial gland. The gland of breeding females is filled with a brown secretion, whereas the empty male's gland is small (Martín-Vivaldi et al. 2009). As an indicator of body condition, we used the residuals of a linear-mixed model with body mass as the dependent variable and sex and body size (defined as the length of primary 5), as independent variables, and individual

identity as random intercept (effect size of primary length $0.32 \text{ g} \pm 0.10 \text{ SE}$, $F_{1,92} = 7.23$, $p = 0.01$, effect size of sex $1.68 \text{ g} \pm 0.93 \text{ SE}$, $F_{1,203} = 3.28$, $p = 0.07$). The sexes differed in body size (mean primary length of males $119.3 \text{ mm} \pm 3.2 \text{ SE}$, $n = 123$, of females $113.5 \text{ mm} \pm 3.7 \text{ SE}$, $n = 175$; linear mixed model: $F_{1,203} = 142$, $p < 0.0001$).

Two age classes were distinguished according to the ringing record or, if not ringed, to the moult pattern. Second-year birds (SY, $n = 145$), breeding for the first time in their life span, were ringed as chicks the previous year or had old, dull primary feathers (SY do not moult their primaries in winter; Cramp 1985). Adults (AD, $n = 153$) were ringed as SY or adults in a previous year or had new, shiny black primary feathers (AD moult their primaries in winter; Cramp 1985).

Corticosterone assay

Total plasma corticosterone concentration (i.e. the free fraction and the fraction bound to corticosteroid-binding globulin) was determined by competitive enzyme immune assay (Munro and Stabenfeldt 1984; Munro and Lasley 1988). A sample of 5–10 μl of plasma diluted with, respectively, 195–190 μl water ($\text{H}_2\text{O}_{\text{bidest}}$) were extracted with 4 ml dichloromethane, re-dissolved in 550 μl phosphate buffer and given in triplicate in the enzyme immune assay. The microplates were coated with a 1:8,000 final dilution of antibody (Chemicon, cross-reactivity: 11-dehydrocorticosterone 0.35 %, progesterone 0.004 %, 18-OH-DOC 0.01 %, cortisol 0.12 %, 18-OH-B 0.02 % and adolsterone 0.06 %). Horseradish peroxidase (HRP, final dilution 1:400'000) conjugated to corticosterone was used as enzyme label and 2,2'-Azino-bis(3-ethylbenzothiazoline-6-sulfonicacid)diammonium salt (ABTS) as substrate. The concentration of corticosterone in plasma samples was calculated by using a standard curve run in duplicate on each plate. If the concentration was below the detection threshold, the value of the lowest detectable concentration was assigned (4 of 338 baseline level determinations). Two plasma pools with low and high corticosterone concentrations were used as internal controls on each plate. Inter-assay variation ranged from 14.4 to 16.8 % and the intra-assay variation ranged from 9.61 to 18.4 %, depending on the concentration of the internal control. The difference in corticosterone levels between years was not due to a corresponding systematic inter-assay variation. The performance characteristics of our assay were: sensitivity 8.8 pg/ml, recovery 76.1–101.9 % and accuracy within 15 %.

Statistical analyses

All statistical analyses were performed using the program R (v.2.14.1, R Development Core Team 2011). To assess

whether the change in corticosterone from baseline levels to handling-induced levels was significant, and whether handling-induced levels of corticosterone differed between the sexes, we conducted a linear-mixed model as implemented in the package nlme (Pinheiro et al. 2011), with corticosterone levels attained after 20–30 min of handling as the dependent variable, blood sample (baseline vs. handling-induced), sex and their interaction as fixed factors and individual identity and pair identity as random intercept.

In order to test whether the adrenocortical stress response varied with the relative brood value, the effects of breeding attempt category, sex and several other factors (see below) on the corticosterone level attained after 20–30 min of handling (dependent variable, ln-transformed to obtain normally distributed residuals) was evaluated with linear-mixed models as implemented in the package nlme (Pinheiro et al. 2011). This procedure is appropriate for the estimation of fixed effects in analyses with repeated measures in an unbalanced design. Individual identity was introduced as random intercept using restricted maximum likelihood estimation and likelihood-ratio for significance testing (Zuur et al. 2009), thus accounting for the fact that 35 % of the individuals were investigated at two breeding attempts. Because one parent may influence the stress response of its partner, we also included pair identity as random intercept.

The significance of the fixed effects was tested sequentially in the order specified in the model with conditional *F* tests (Pinheiro and Bates 2000). This method is appropriate for correlated independent variables sequentially introduced into the model in a biologically meaningful sequence. We first introduced baseline corticosterone, time after capture, time of day and study year that could mask other effects. We corrected baseline levels to a common time between capture and blood sampling of 120 s, because we observed a significant increase of corticosterone within the first 3 min after capture [effect of handling time (min): 1.9 ng/ml \pm 0.3 SE, $F_{1,74} = 44$, $p < 0.0001$]. Then, we introduced the variables of main interest: sex, age of the parent, age of the chicks, brood size, body condition, breeding attempt category and day of year. We included all two-way interactions between sex, breeding attempt and day of year (see Table 1 for the full model). The effect sizes are given for the full model. The graphs present estimates of the reduced model, i.e. with all non-significant terms removed.

It is unclear whether the corticosterone levels attained at a certain time after handling (e.g. 25 min) or the increase in corticosterone from baseline to the handling-induced level at a certain time is physiologically relevant. We therefore repeated this analysis in two ways. First, we repeated the analysis without baseline corticosterone concentration as an explanatory variable. Second, we used the difference between handling-induced and baseline levels of

corticosterone as the dependent variable. These two additional analyses did not substantially change the results presented in Table 1 and are reported in the Electronic Supplementary Material (ESM).

The dependence of fledging success and rearing success on handling-induced corticosterone levels was examined with a generalised linear model using a Poisson or a quasi-binomial distribution, respectively. Both handling-induced corticosterone levels of the male and of the female of a brood were the independent variables together with hatching date. Because male and female of the same brood may differ in breeding attempt category (e.g. a male having its second brood with a first-breeder female), we chose hatching date and not breeding attempt category as the explanatory variable to account for seasonal effects. Chi square was used for significance tests of the single terms and terms with $p > 0.05$ were eliminated from the model.

The effect of handling-induced corticosterone level on survival was analysed with a logistic regression with quasi-binomial distribution, using the recapture events in the year following blood sampling as the binary dependent variable (the bird was either recaptured or not) and corticosterone level, sex and their interaction as independent variables. Because recapture rate was high (82 %), it was justified to use a logistic regression and there was no need to apply capture-recapture statistics. Chi square was used for significance tests of the single terms. We averaged the handling-induced corticosterone levels of birds blood sampled twice within the same year. Alternatively, we also used the blood sample of the first or the second brood for individuals sampled during two breeding attempts with very similar results.

Results

Handling-induced corticosterone levels and brood value

Handling-induced corticosterone levels ranged widely between 7.70 and 73.25 ng/ml. The increase of corticosterone levels between the first (baseline) and the second (handling-induced) blood sample 20–30 min after capture was highly significant, but smaller in females than in males (linear-mixed model with individual identity as random factor: intercept: 9.34 ng/ml \pm 0.87 SE; difference between baseline and handling-induced samples: 24.60 ng/ml \pm 1.08, $F_{1,389} = 1,006$, $p < 0.0001$; difference between sexes: -0.26 ng/ml \pm 1.13, $F_{1,203} = 7.3$, $p = 0.0075$; interaction term: -4.30 ng/ml \pm 1.41, $F_{1,389} = 9.3$, $p = 0.0025$; the random intercept individual identity was significant: LR = 14.37, $p < 0.0001$).

Handling-induced corticosterone levels were dependent on baseline corticosterone, time of day, study year, sex,

Table 1 Dependence of handling-induced total corticosterone levels in Eurasian hoopoes *Upupa epops* (ln-transformed, $n = 298$) on various factors in a linear mixed model (individual identity as random factor, $n = 205$, LR = 19.87, $p < 0.001$)

Variable	Effect \pm SE	df	F value	p value
Intercept	4.37 \pm 0.90	1; 203	16,000	0.0001
Baseline corticosterone	0.0286 \pm 0.0073	1; 74	33.60	0.0001
Time since capture	-0.00002 \pm 0.00018	1; 74	12.52	0.0007
Time of day	-0.00023 \pm 0.00013	1; 74	5.46	0.022
Year (2008)	-0.158 \pm 0.052	1; 74	5.43	0.023
Sex (female)	0.062 \pm 0.599	1; 203	7.19	0.0080
Age of parent (AD)	0.048 \pm 0.051	1; 74	2.91	0.093
Brood age	0.0035 \pm 0.0072	1; 74	0.16	0.69
Brood size	0.0020 \pm 0.01370	1; 74	1.60	0.21
Body mass residual	-0.0109 \pm 0.0046	1; 74	3.13	0.081
Breeding attempt		3; 74	3.63	0.017
2	-1.879 \pm 0.823			
1a	0.706 \pm 0.904			
1b	0.445 \pm 1.184			
Julian day	-0.007 \pm 0.006	1; 74	2.74	0.10
Sex (female) \times breeding attempt		3; 74	0.73	0.54
2	0.031 \pm 0.203			
1a	-0.053 \pm 0.122			
1b	-0.160 \pm 0.221			
Sex (female): Julian day	-0.001 \pm 0.004	1; 74	0.55	0.46
Breeding attempt \times Julian day		3; 74	4.14	0.0090
2	0.0112 \pm 0.0054			
1a	-0.0049 \pm 0.0063			
1b	-0.0016 \pm 0.0073			

p values are given when sequentially adding the variables. Effect sizes are for the full model. When non-significant terms were eliminated from the model (reduced model, used for producing Figs. 1, 2), significant terms (in bold) remained significant, except for time since capture

body condition and breeding attempt category in interaction with sampling date, but not on brood size or age of the adults (Table 1). Pair identity as random effect was not significant ($p = 0.7$) and was therefore removed from the model presented in Table 1. Time since capture was significant when introduced as the second variable in the model, but had no effect in the final model (standard error much larger than effect size; Table 1). Handling-induced corticosterone levels decreased slightly over the day [e.g. from 47.23 (0.95 CI: 25.81; 88.08) at 0900 hours to 43.52 ng/ml (23.86; 80.74) at 1500 hours; model estimates for females with an average body condition during breeding attempt category 1a in 2008 at mean time since capture and mean day of year; same decrease in males and the other breeding attempt categories] and were higher in 2007 than in 2008 [e.g. 29.01 ng/ml (0.95 CI: 25.88; 32.51) in 2007 and 25.53 ng/ml (23.08; 28.22) in 2008; model estimates for females of breeding attempt category 1a at mean time since capture and mean day time and average body condition; same difference between years in males and the other breeding attempt categories]. Handling-induced

levels of corticosterone were significantly higher in males than in females [e.g. 30.27 ng/ml (0.95 CI: 27.18; 33.69) in males and 25.53 ng/ml (23.08; 28.22) in females; model estimates for breeding attempt category 1a in 2008 at mean time since capture, day time and body condition, same difference between the sexes in the other breeding attempt categories, see Fig. 1], and decreased with increasing body condition [e.g. 26.50 ng/ml (0.95 CI: 23.79; 29.57) at the first quartile of the frequency distribution of the body condition and 24.65 ng/ml (22.28; 27.35) at the third quartile of the frequency distribution of the body condition; model estimates for females of breeding attempt category 1a in 2008 at mean time since capture and day time].

During early broods (breeding attempt categories 1 and 1a) handling-induced corticosterone levels were higher than during late broods (categories 2 and 1b; Fig. 1). Post-hoc Welch t tests showed significant differences in mean handling-induced corticosterone levels between breeding attempt categories 1 and 2 ($t = 2.8$, $p = 0.006$) or categories 1 and 1b ($t = 3.3$, $p = 0.001$), but not between the other breeding categories ($t < 1.9$, $p > 0.06$). During early

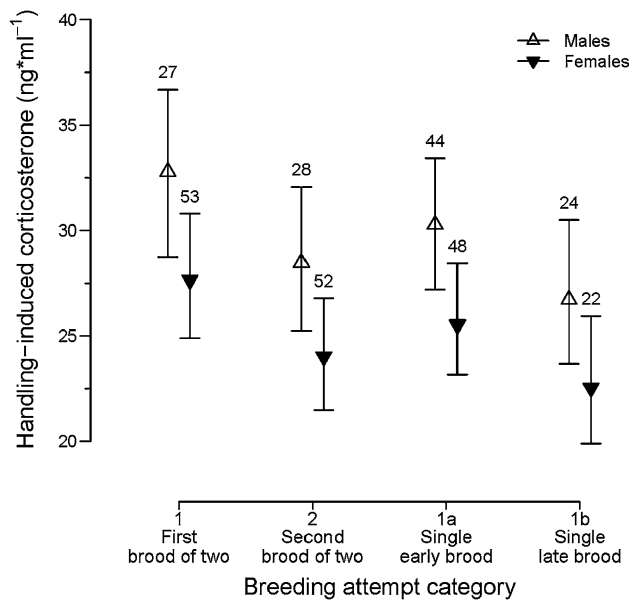


Fig. 1 Dependence of handling-induced total corticosterone levels on breeding attempt category for male (empty pointing-up triangles) and female (filled pointing-down triangles) Eurasian hoopoes *Upupa epops*. The back-transformed predicted means and 95 % confidence intervals were computed for the mean time since capture (23 min) and sampling time of day (1204 hours) in year 2008, average body condition and average base-line corticosterone from the reduced model given in Table 1. Numbers indicate sample sizes

broods (categories 1 and 1a), handling-induced corticosterone levels significantly decreased with ongoing date ($F_{1,170} = 8.3, p = 0.005$), while there was no dependence on date during late broods (categories 2 and 1b: $F_{1,124} = 2.2, p > 0.1$; Fig. 2). The non-significance of date for late breeders was due to the fact that birds attempting their first brood of the year (category 1b) tended to reduce their stress response with ongoing date, whereas birds attempting their second brood of the year (category 2) showed an increase of handling-induced corticosterone levels with ongoing date (Fig. 2; significant interaction breeding attempt \times date, $p = 0.01$, Table 1).

Reproductive success and return rate

Fledging success was related to hatching date and handling-induced corticosterone levels of the female (final model; intercept: 3.28 ± 0.29 SE; hatching date effect: $-0.011 \pm 0.002, p_{\text{Chi}} < 0.001$; corticosterone effect: $-0.007 \pm 0.003, p_{\text{Chi}} = 0.014$; Fig. 3), while handling-induced corticosterone level of the male ($p_{\text{Chi}} = 0.84$) and its interaction with handling-induced corticosterone level of the female ($p_{\text{Chi}} = 0.61$) were not significant and eliminated from the final model. Fledging success decreased during the breeding season and females with an attenuated stress response had a higher fledging success than females with a strong stress

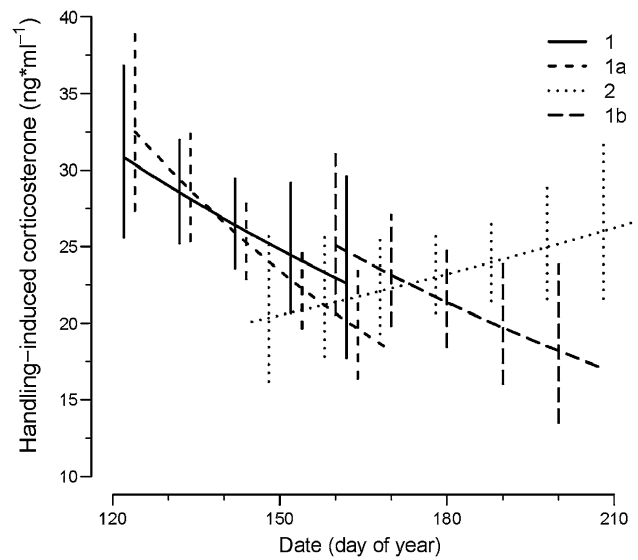


Fig. 2 Dependence of handling-induced corticosterone levels on day of year (since 1 January) and breeding attempt category ($n_1 = 80, n_{1a} = 92, n_2 = 80, n_{1b} = 46$). The slopes predicted from the model [see text, Table 1, computed for the mean time since capture (23 min) and sampling time of day (1204 hours) in year 2008, average body condition and average base-line corticosterone] are given with 95 % confidence intervals drawn at regular intervals. Breeding attempt categories are indicated: 1 first brood of two, 2 second brood of two, 1a single early brood, 1b single late brood

response. For both sexes, fledging success did not depend on body condition (logistic regression, $n = 198$ broods, $p_{\text{Chi}} > 0.08$) and did not differ between the two study years (logistic regression, $n = 198$ broods, $p_{\text{Chi}} > 0.88$).

Rearing success (the proportion of eggs that produced fledglings) was related to hatching date and handling-induced corticosterone levels of the female (final model; intercept: 3.006 ± 0.668 SE; hatching date effect: $-0.015 \pm 0.004, p_{\text{Chi}} < 0.001$; corticosterone effect: $-0.014 \pm 0.007, p_{\text{Chi}} = 0.022$; Fig. 3), while handling-induced corticosterone level of the male ($p_{\text{Chi}} = 0.96$) and its interaction with handling-induced corticosterone level of the female ($p_{\text{Chi}} = 0.46$) were not significant and eliminated from the final model. Rearing success decreased during the breeding season and females with an attenuated stress response had a higher rearing success than females with a strong stress response. For both sexes, rearing success did not depend on body condition and did not differ between the two study years (logistic regression, $n = 198$ broods, $p_{\text{Chi}} > 0.25$).

The probability of recapture during the subsequent breeding season (i.e. in the year after blood sampling) was almost significantly dependent on handling-induced corticosterone levels in interaction with sex (interaction term handling-induced corticosterone \times sex: $p_{\text{Chi}} = 0.05$), but was not dependent on handling-induced corticosterone levels when both sexes were analysed separately (male:

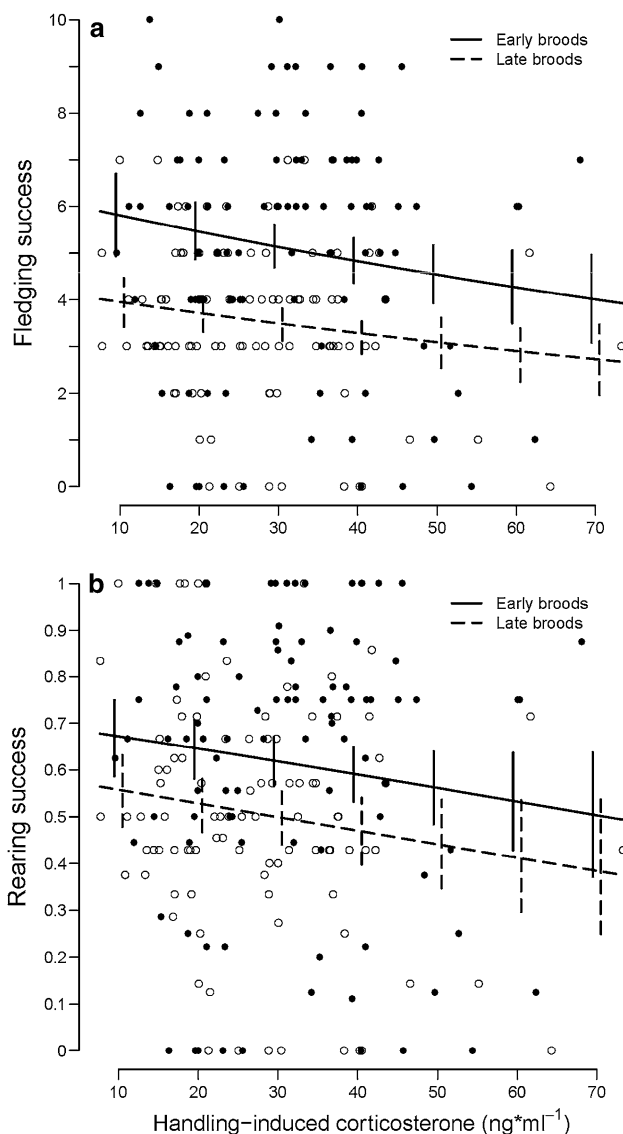


Fig. 3 Dependence of fledging success (**a**) and rearing success (**b**; proportion of eggs that produced fledglings) on handling-induced total corticosterone levels of females for early (dots birds captured before day of year 145) and late broods (circles birds captured after day of year 145). The slopes predicted from the model (see text) are given with 95 % confidence intervals drawn at regular intervals and refer to day of year 130 for early broods and day of year 169 for late broods

$p_{\text{Chi}} = 0.1$; female: $p_{\text{Chi}} = 0.2$). Return rate tended to be positively correlated with handling-induced corticosterone in males but negatively correlated in females. If the handling-induced corticosterone level during the first brood (or alternatively the second brood) was used in birds caught during two breeding attempts, there was also no significant relationship with return rate (males and females combined or analysed separately, all $p > 0.7$). Return rates were not correlated with rearing success, either in males ($p_{\text{Chi}} > 0.94$) or in females ($p_{\text{Chi}} > 0.34$).

Discussion

In this study, we showed in a short-lived multi-brooded bird that the naturally occurring adrenocortical response to acute stress varied with breeding attempt and sex as predicted by the brood-value hypothesis. A high adrenocortical stress response was correlated with a low fledging and rearing success in females, which is also predicted by the brood-value hypothesis. Return rate, as a measure of apparent survival, was not clearly correlated with the adrenocortical stress response, although such a positive relationship would be predicted by the brood-value hypothesis.

Stress response and brood value

Individuals during their first of two breeding attempts had a higher adrenocortical stress response than during their second broods (Fig. 1). This is evidence in support of a within-individual modulation of the stress response and corroborates the experimental findings in multibrooded house sparrows *Passer domesticus* (Lendvai et al. 2007; Lendvai and Chastel 2008). These authors could demonstrate with brood manipulation and mate removal experiments that the adrenocortical response to acute stress is adapted to the brood value, with an up-regulation when the brood loses value but a down-regulation when the brood gains value. Within the early breeding hoopoes, there was a decrease in adrenocortical stress response with ongoing date, while this was not the case in late-breeding birds (second breeders instead showed an increase; Fig. 2). Very similar effects were observed in house sparrows (Lendvai et al. 2007). This is evidence for between-individual differences in adrenocortical stress response according to breeding attempt and the timing of breeding.

These within-individual modulations and between-individual differences in stress response are in accordance with the brood-value hypothesis. The hoopoe is a short-lived migratory bird with an annual apparent survival of only 38 % in the study population (Schaub et al. 2012). Missing the current year of reproduction therefore entails a high probability of never reproducing in the future. The relative value of the brood increases with ongoing breeding season, because the probability of laying another clutch during the same breeding season decreases. Therefore, late breeders without a chance to rebreed during the same season should maximise their current reproduction to increase their lifetime reproductive fitness and hence reduce the stress response. After about mid-June (day of year 165), time is too short to produce another brood in the same year and hence relative brood value does not increase any further, but has reached its highest value. This would explain why the adrenocortical stress response did not decrease further

after mid-June (day of year 165; Fig. 2). In birds during their second of two broods, the stress response even increased, as also observed in the house sparrow (Lendvai et al. 2007). This might indicate that the value of the brood decreased again towards the end of the breeding season, because survival of late-born young might be low at the end of the breeding season, as observed in many species (e.g. Gruebler and Naef-Daenzer 2008; Low and Pärt 2009). Indeed, only 9 % of late broods (category 2 and 1b) had at least one chick returning the next year to the study area, while this figure was 25 % for early broods (category 1 and 1a) (own unpublished data).

As is typical for correlative studies, alternative explanations may exist for the between-individual differences in stress response. A first explanation is that late breeders are younger (which is the case: first breeders breed on average 7 days later than experienced breeders: first breeders day of year 146 ± 17 SD; experienced breeders 139 ± 16) and hence may have a higher residual lifespan and thus a lower brood value of the current brood and, according to theory, a higher stress response than early breeders which are older. However, we observed a lower stress response in late breeders (Fig. 1). A second explanation is that late breeders are of lower quality (which is often the case in birds) and hence will have a different adrenocortical stress response than high-quality individuals, independently of their brood value. The question is whether low-quality individuals have a lower or higher stress response than high-quality individuals. If low individual quality translates into low rearing success, our study demonstrated a higher stress response than in high-quality individuals. However, we found a lower, not higher, stress response in late breeders (Fig. 1). A third explanation is that the decrease in stress response from early to late broods is part of the seasonal variation in stress response. The adrenocortical stress response varies considerably over the annual cycle and is low during postbreeding moult (Romero 2002). Therefore, the decrease towards the end of the breeding season might anticipate the presumed low stress response during the partial moult which starts after the last brood has fledged (Cramp 1985). However, in this case, we would expect the very latest breeders to attenuate their stress response, while we observed an unchanged or even increasing stress response during the second half of the breeding period (Fig. 2). Moreover, we did not observe an overlap between chick rearing and moult.

As a response to handling, females had a significantly lower total corticosterone release than males. In the hoopoe, parental care between the sexes is highly asymmetric, depending on the breeding phase (Arlettaz et al. 2010b). Only the female invests in egg production, incubation and brooding of chicks up to 8–10 days of age, while being fed by the male. In turn, the male invests much more in

provisioning, while the female may even leave the brood during the last phase of provisioning to engage in a new breeding attempt (Arlettaz et al. 2010b). Given these sex-specific discrepancies in parental care, it is difficult to effectively calibrate the relative effort of each sex. However, several studies have found a lower stress response in the sex providing more parental care and this has been regarded as supporting the brood-value hypothesis (reviewed in Bókony et al. 2009). In our study population, extra-pair paternity occurs in an estimated 4 % of broods (Berthier et al. 2012; similar to Spain: 10 % of broods; Martín-Vivaldi et al. 2002), whereas conspecific brood parasitism might affect up to 7 % of broods (Berthier et al. 2012). Thus, since extra-pair paternity and conspecific brood parasitism are supposed to decrease the intrinsic value of the brood for the male, this could explain why we observed a stronger adrenocortical stress response in males compared to females. Only behavioural studies can put forward more precise predictions regarding the brood-value hypothesis, taking into account individual parental investment.

Handling-induced levels of corticosterone were higher in 2007 than in 2008. In 2007, rainfall was abnormally high during the breeding season (monthly rainfall during daytime for 2007 vs. 2008: May 50 vs. 2 mm; June 43 vs. 8 mm; July 30 vs. 17 mm; data from MeteoSchweiz) and rainfall has a negative impact on reproductive output (Arlettaz et al. 2010b). Indeed, reproductive output in 2007 was lower than in 2008 (number of broods with at least one egg laid 165 vs. 121; mean number of fledglings 3.19 vs. 3.93; unpublished data), mainly due to broods abandoned during their early phase, while rearing success of the broods, as used in this study, did not differ between the 2 years. Hence, the probability of raising a brood successfully might have been felt by the birds as being lower in 2007 than in 2008, and hence also the relative brood value. One possible explanation is that the higher handling-induced levels of corticosterone in the year 2007 compared to 2008 would reflect worse breeding conditions.

Stress response, reproductive success and survival

We observed a negative correlation between fledgling success or rearing success and handling-induced corticosterone levels in females, but not in males. Rearing success (the proportion of eggs that produced fledglings) predominantly depends on incubation and food provisioning, because nest predation is nearly nonexistent in hoopoe study population (own observations).

To our knowledge, our study provides the first evidence that the strength of the natural adrenocortical response to an acute stressor is related to breeding success in birds. This relationship was not very strong (although highly

significant), which was to be expected when relating a point measure in time (corticosterone) to a process taking several weeks (rearing chicks). There are different explanations for the finding that this relationship only held for females and not for males. Although male investment in reproduction may be energetically more demanding, it may still be that female quality and behaviour govern the outcome of reproduction, particularly during the sensitive phase of the first days of life of the chicks. Most losses occur around hatching and during the subsequent days when females attend the brood (Arlettaz et al. 2010b). Therefore, a high female stress response may be more deleterious to the brood than a high male stress response. Breeding white-crowned sparrows *Zonotrichia leucophrys* forced to leave the breeding site because of snow storms had high corticosterone levels as a response to this acute stressor, and individuals with the highest levels delayed their return to the breeding site compared to birds with lower corticosterone levels (Breuner and Hahn 2003). We may therefore infer that females mounting a strong adrenocortical response to an acute stressor had reduced nest attendance. For instance, they may delay their return to the nest after incubation and brooding breaks, which would compromise embryo and chick development. In addition, hoopoe females of this population had higher baseline prolactin levels than males (Schmid et al. 2011), indicating a stronger bond of the female to the nest than of the male (Angelier and Chastel 2009). Further behavioural studies are needed to test this hypothesis. It also remains to be shown whether the observed relationship between rearing success and stress response is due to an individual modulation of the stress response or whether it is due to basic differences in stress response between individuals. In this study, we compared inter-individual differences in reproductive success and therefore cannot distinguish between the two alternatives. Moreover, environmental conditions could affect both the HPA-axis responsiveness and rearing success independently, without a causal affect of corticosterone on rearing success.

Although we found a negative relationship between stress response and rearing success, we did not find a clear positive correlation with survival (expressed as return rate), as predicted by the brood-value hypothesis. Three explanations may account for this observation. First, the return rate over 1 year may not be a good measure of true survival, because it may include an appreciable, but unknown, proportion of birds emigrating from the study area (see Bötsch et al. 2012). Second, the relationship between survival and adrenocortical stress response may be dependent on environmental conditions. Birds in more strenuous environmental conditions may benefit from a higher stress response in terms of survival, while the survival of birds in benign conditions may be governed by other factors

(Angelier et al. 2009b). We might have had an appreciable part of our birds living in conditions that did not entail a positive relationship between survival and stress response. Third, there was no negative correlation between rearing or fledging success and return rate which we would expect under the assumption of a trade-off between current reproduction versus survival and future reproduction. In contrast, a detailed analysis of 8 years of data revealed a positive relationship between current reproductive output and future apparent survival (Bötsch et al. 2012). This result is unlikely to originate only from increased emigration of unsuccessful breeders. It is likely that this positive relationship between reproductive output and future survival is due to differences in individual quality, i.e. high-quality individuals having both a high reproductive output and a high survival and low-quality individuals having a low reproductive output and a low survival.

Conclusions and perspectives

This correlational study in free-living birds provides support for the brood-value hypothesis in that we found variation in the stress response with breeding attempt, sex and reproductive success, as predicted by life-history theory. However, we did not find the expected relationship between stress response and apparent survival.

Further studies may address two so far understudied aspects of the brood-value hypothesis. First, the effects of corticosterone as a response to an acute stressor are most probably mediated by the biologically active free fraction of corticosterone, rather than the fraction bound to corticosteroid-binding globulin (CBG) or total corticosterone concentration, as used in this study (Malisch and Breuner 2010). Therefore, further studies should investigate the level of free corticosterone, because CBG may withhold a variable fraction of total corticosterone which can serve as a reservoir. We are aware of only one study that looked at CBG capacity and free corticosterone in the context of the brood-value hypothesis (Breuner et al. 2003). This study showed that total handling-induced corticosterone levels did not vary between populations of white-crowned sparrows with different numbers of annual broods, whereas CBG and hence free corticosterone did.

Second, correlative cross-sectional (i.e. between-individual) studies notoriously lack the power of revealing individual-based mechanisms, such as internal modulation of hormone secretion. Many studies claiming to support the brood-value hypothesis or the existence of a relationship between stress response and measures of fitness (survival, reproductive success; Breuner et al. 2008) actually refer to between-individual variation. However, between-individual studies cannot readily reveal within-individual

decisions and mechanisms without taking into account individual differences (van Noordwijk and de Jong 1986). Both approaches have their merits, but should not be confounded.

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