PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

# Predicting reproductive success from hormone concentrations in the common tern (*Sterna hirundo*) while considering food abundance

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**Abstract** In birds, reproductive success is mainly a function of skill or environmental conditions, but it can also be linked to hormone concentrations due to their effect on behavior and individual decisions made during reproduction. For example, a high prolactin concentration is required to express parental behaviors such as incubation or guarding and feeding the young. Corticosterone level, on the other hand, is related to energy allocation or stress and foraging or provisioning effort. In this study, we measured individual baseline prolactin and corticosterone between 2006 and 2012 in breeding common terns (*Sterna hirundo*) using blood-sucking bugs. Reproductive parameters as well as prey abundance on a local and a wider scale were also determined during this period. Baseline prolactin and corticosterone varied significantly between years, as did breeding success. At the individual level, prolactin was positively and corticosterone was negatively linked to herring and sprat abundance. At the population level, we also found a negative link between corticosterone and prey abundance, probably reflecting overall foraging conditions. High prolactin during incubation was mainly predictive of increased hatching success, potentially by supporting more constant incubation and nest-guarding behavior. It was also positively linked to a lesser extent with fledging success, which could indicate a high feeding rate of young. Corticosterone concentration was positively related to high breeding success, which may be due to increased foraging activity and feeding of young. In general, our study shows that baseline prolactin and corticosterone levels during incubation can predict reproductive success, despite the presence of an interval between sampling and hatching or fledging of young.

**Keywords** Prolactin · Corticosterone · Breeding success · Year effect · Food abundance

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## Introduction

Energy allocation between competing life-history traits, especially under challenging conditions, is a key factor determining fitness (McNamara and Buchanan 2005). While breeding, parents face a trade-off between investment in offspring and self-maintenance (Stearns 1992). Especially in long-lived species, parental care should be reduced if food abundance decreases and body condition deteriorates considerably, so as not to compromise their future survival and reproduction (Stearns 1992; Wingfield et al. 1998). Reproductive behavior and life-history trade-offs are largely mediated by hormones (Sinervo and Svennson 1998; Angelier and Chastel 2009), linking the individual and its body state to environmental conditions (Doody et al. 2008) and optimizing its behavior.

Corticosterone, the main avian glucocorticoid, increases rapidly under stressful conditions (Romero and Romero 2002; Romero and Reed 2005), and is involved in homeostatic energy balance, which mediates energy allocation

during reproduction (Wingfield and Sapolsky 2003). High corticosterone concentrations are often found to be linked with low food abundance in seabirds (Kitaysky et al. 1999, 2007; Buck et al. 2007; Doody et al. 2008) and low reproductive success (reviewed in Bonier et al. 2009a). Furthermore, experimentally increased food supply can decrease baseline corticosterone secretion (Lanctot et al. 2003). However, aside from this often-emphasized negative effect of corticosterone on reproduction, a short term elevation in baseline corticosterone supports adaptive mobilization of energy stores (reviewed in McEwen and Wingfield 2003) and stimulates foraging effort (Angelier et al. 2007a). This leads to increased parental body mass or even to a higher feeding rate of young (Doody et al. 2008, Bonier et al. 2009b), especially when parents are in good body condition.

Corticosterone may affect parental behavior via a link with prolactin, a pituitary hormone that is involved in the initiation and maintenance of parental care (reviewed in Buntin 1996). High levels of prolactin enhance incubation, nest defence, and brood guarding (Wang and Buntin 1999), and may be directly linked to the amount of parental care (reviewed in Angelier and Chastel 2009). Laboratory studies in ring doves (*Streptopelia risoria*) and turkey hens (*Meleagris gallopavo*) revealed that injection of prolactin stimulates the expression of feeding, brooding, and protective behavior (Buntin et al. 1991; Youngren et al. 1991; Wang and Buntin 1999). Further evidence for the role of prolactin comes from Sharp et al. (1989) and El Halawani et al. (1995), who found that an experimental reduction in circulating prolactin in turkeys and domestic hens leads to inhibition of incubation behavior. Finally, experimentally reducing the prolactin concentration results in lowered alloparental behavior of king penguins *Aptenodytes forsterii* (Angelier et al. 2006). The prolactin titer is also sensitive to a decline in body mass: low body mass was found to be related to a decreased prolactin level, especially in birds in poor body condition (Criscuolo et al. 2002, 2003; O'Dwyer et al. 2006). Moreover, experimentally increasing the corticosterone concentration can result in a decreased prolactin level (Angelier et al. 2009), which lowers nest attendance and provisioning of young (Spee et al. 2010). Acute stress often leads to a decrease in prolactin concentration (Chastel et al. 2005; Angelier and Chastel 2009), and some studies have found evidence that prolactin and corticosterone are mechanistically linked, at least during a prolonged period when stressors are present (Angelier and Chastel 2009).

As reproductive success in vertebrates is largely driven by food availability (Golet et al. 2004), many studies have found a negative relationship between baseline corticosterone and reproductive success in seabirds (Buck et al. 2007; Angelier et al. 2010; Kitaysky et al. 2010). However, this is generally time- and state-dependent, and no effects of or positive links between corticosterone and reproductive success are reported (the cort-fitness hypothesis, Bonier et al. 2009a; the cort-adaptation hypothesis, Bonier et al. 2009b; the context-dependent hypothesis, Bonier et al. 2013). Prolactin level may be related to reproductive success in birds, with high levels increasing breeding success (Duckworth et al. 2003; Ouyang et al. 2011) due to more constant incubation, nest guarding, and increased provisioning of young (Wang and Buntin 1999).

We investigated the relationships between different parameters of reproductive success (hatching, fledging, breeding success) and baseline prolactin and corticosterone levels in a small, long-lived seabird, the common tern (*Sterna hirundo*) during a multi-year survey. Blood samples were taken in the middle of the individual incubation period (between 9 and 14 days after clutch completion) to avoid the relation between success and hormones being confounded by differences in individual progress in the breeding cycle. The aims of our study were (1) to investigate annual differences in baseline prolactin and corticosterone levels, (2) to assess if prolactin and corticosterone baseline concentrations were related at the population level to the output of the incubation or rearing period (expressed as hatching and fledging success), (3) to assess how prey abundance is linked to hormone values at the population and individual level, and (4) to test if relationships between hormones and reproductive success are also detectable at the individual level.

## Materials and methods

### Studied colony

Field work was done between 2006 and 2012 in a common tern colony in Wilhelmshaven, northern Germany (53°30′40″N, 8°06′20″E). The common terns breed on six artificial islands, and behavior and reproductive success had been studied since 1984. Each island (11 × 5 m) is surrounded by a low wall to prevent flooding and entry of terrestrial predators. The islands are separated from each other by about 1 m. All fledglings are marked with a metal ring and (since 1992) are additionally fitted with a subcutaneously injected microchip (transponder). During their whole lives, these marked individuals are automatically and remotely recorded within the colony by special antennae in resting boxes that are placed on the walls of the islands (for details see Becker and Wendeln 1997). The antennae record individual transponder codes every 5 s, and these data are saved on the computer together with time of day. Between 1992 and 1995, 101 adults were additionally caught on their nests and fitted with transponders. Since 1998, all fledglings in the colony have been sexed by molecular methods (Becker and Wink 2002), while older birds have been sexed by observing copulations.

The number of breeding pairs in the colony ranged from 355 in 2009 to 470 in 2006 during the study period (2006–2012). Each nest was equipped with a mobile antenna for about 1 day during incubation to identify transponder-marked birds and pair mates.

To determine the parameters of breeding success, the colony was checked three times a week, new nests were located, and eggs were labeled according to laying order (for details see Wagener 1998). The fate of the eggs and hatchlings was monitored at each subsequent check until fledging (which occurred on average at 27 days old, Becker and Wink 2002) to determine the hatching and fledging success for each pair.

Measuring prey abundance

We used two approaches to determine food abundance. First, we included a yearly mean index for herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) abundance in the whole North Sea extracted from the ICES (2013) HAWG report (http://www.ices.dk/reports). These indices correspond to the reproductive performance of common terns at the "Banter See" colony (Dänhardt and Becker 2011a). For herring, we used the estimated population abundances of age group 0 and age group 1 (see ICES report 2013, p. 115), as adult and young common terns feed mainly on these (Becker and Ludwigs 2004; Dänhardt and Becker 2008; Diamond et al., unpubl.). Since all age classes of sprat are potentially caught by common terns, we included the total number of sprat in the analyses (obtained from the first quarter International Bottom Trawl Survey, ICES 2013). See Online Resource 1 in the Electronic supplementary material (ESM) for the abundance index values. Because common terns from the colony mainly forage at Jade Bay near the colony (southeast of Wilhelmshaven, Germany), this measure of food abundance in the whole North Sea may be not very accurate. Hence, second, we estimated local herring abundance in Jade Bay near the research colony because herring is one of the most important food sources of the common terns breeding at the research colony (Becker and Ludwigs 2004, Dänhardt and Becker 2011a). Herring abundance was determined at the cooling water intake of a power plant in Wilhelmshaven at a distance of only about 8 km from the colony. The cooling water is absorbed from the water body of Jade Bay, including prey species (which are retained by trash screens). We specified, counted, and collected all marine organisms in a large chute 1–4 times per month during 2 h of ebb tide in a standardized setup (for details see Dänhardt and Becker 2008). Only individual herrings with lengths of up to 15 cm were included in these analyses because those are used by common terns as prey. Food abundance was described in number of individuals per 10,000 $m^3$ water and the mean

number of herring per month was then used for our analyses. We investigated data from April and May, when common terns start courtship and egg-laying, and when blood samples of breeders were taken (May).

Blood sampling

Blood samples of incubating common terns were taken minimally invasively by using starved third stages of blood-sucking bugs (*Dipetalogaster maxima*) in artificial hollow eggs. After identifying the incubating bird via a mobile antenna on the nest, the whole clutch was replaced by artificial eggs, one containing the hungry bug (for details see Becker et al. 2006; Riechert et al. 2012). After 20–30 min, the bugs were checked and the sampling process was usually finished and the blood was extracted from the bug into a syringe. The bugs had succeeded in sucking blood in at least 80 % of trials throughout the whole sampling period (mean 87 %, range 80–99 %). Among other parameters, this method was successfully validated for baseline prolactin (Riechert et al. 2012) and corticosterone levels (Arnold et al. 2008).

Terns were sampled in the middle of their individual incubation period (9–14 days after clutch completion). In none of the analyzed years was baseline prolactin or corticosterone level significantly related to the day of sampling after clutch completion ($-0.1 < r_s < 0.2$, $P > 0.1$ in every case, $65 < N < 217$). Sampling was done in the early morning (5 a.m. to 10 a.m.). We did not find a significant correlation between baseline prolactin and time of day during most years ($0 < r_s < 0.2$, $P > 0.1$ in every case, $65 < N < 217$). However, prolactin titer was significantly positively related to time of day in 2009 ($r_s = 0.354$, $P < 0.001$, $N = 123$). There was also a significant negative correlation of baseline corticosterone with time of day in 2009 ($r_s = -0.207$, $P = 0.023$, $N = 121$) and 2011 ($r_s = -0.328$, $P = 0.001$, $N = 104$), but the relationship was not significant in any other year ($-0.2 < r_s < 0.2$, $P > 0.05$ in every case, $66 < N < 196$).

Hormone assay

Baseline concentrations of prolactin and corticosterone were determined in the Centre d'Etudes Biologiques de Chizé, France. The method of determining plasma prolactin concentration was validated for this species and study site (Riechert et al. 2012), and resulted in a dose-dependent response curve parallel to the one for standard chicken plasma (source: Dr. A.F. Parlow, UCLA Medical Center, Los Angeles, CA, USA). Baseline prolactin level was analyzed twice in each sample by heterologous radioimmunoassay (RIA). The plasma baseline level of corticosterone was measured in the remaining plasma (usually 25 µl) via

RIA following Lormée et al. (2003). The minimal detectable corticosterone level was around 0.5 ng/ml throughout the years (lowest measurement: 0.84 ng/ml). Due to large sample sizes in some years, samples were run in different assays. However, assay identity did not have a significant effect on baseline prolactin or corticosterone (Riechert et al. 2012). Intra- and inter-assay variation for baseline prolactin and corticosterone was within the range 4–13 % ($N = 4$ duplicates for intra-assay variation).

### Definitions and statistics

We used three parameters of reproductive success. The first was hatching success, which is defined as the proportion of hatchlings from all eggs laid, indicating the quality of the incubation period. The second was fledging success, which describes the proportion of fledglings from hatchlings (including only nests with at least one hatchling), measuring the quality of the rearing period separately. This parameter also includes chicks that fledged but died some time afterwards. The third parameter was breeding success, defined as the number of fledglings per pair. This is a measure of success for the whole breeding period, also including the post-fledging phase, when common terns still feed their young. Furthermore, we created additional groups for the generalized linear model relating to the success parameters: for every parameter, we divided birds into successful ones with at least one hatchling/fledgling/surviving fledgling chick per pair (derived from hatching, fledging, and breeding success, respectively) and unsuccessful ones.

Baseline hormone concentration and the three success parameters were compared between years using a Kruskal–Wallis test, because they were not normally distributed. Post-hoc comparisons were done using Mann–Whitney $U$ tests. The mean baseline prolactin and corticosterone levels for each year (colony means) were related to the mean reproductive success parameters using a Pearson correlation test. We also related baseline prolactin and corticosterone concentrations as well as hatching, fledging, and breeding success to each other and to hormone levels.

We determined the difference in hormone titers and reproductive success parameters in repeatedly sampled individuals from the first year of sampling to the next one. Next, we checked for correlations between the differences in hormone levels and the differences in success rates in both males and females using Pearson correlation tests. Hormone titers of pair mates were also related using Pearson (for prolactin) and Spearman (for corticosterone) correlations. For each single year, we correlated hormone levels and success parameters for males and females separately by the Spearman correlation. Prey abundance in the North Sea (NS) and Jade Bay (JB) were also tested for correlation by Pearson test and linked with mean breeding success during all of the years analyzed.

To analyze different effects on hormone values, we used a general linear mixed model with baseline prolactin or corticosterone as response variable, sex and fish abundance as fixed factors, and nest, year, and ID of birds as random effects, including all two-way interaction terms. We identified suitable models to predict hormone concentrations by an information-theoretic approach (Burnham and Anderson 2002). We used the Akaike information criterion (AIC) and calculated $\Delta$AIC and Akaike's weight ($W_i$) to determine the most suitable models. The model with the lowest AIC was considered to be the best one; models with $\Delta$AIC < 2 compared to the best model were suggested to have substantial support from the data. We excluded all models with $\Delta$AIC > 4 because they are considered to have quite low support according to the current data (Burnham and Anderson 2002).

Two sets of models were calculated for each hormone, one with herring (age class 0 and 1) and sprat abundances in the North Sea (these abundances were termed A-NS-H0, A-NS-H1, and A-NS-S, respectively), and one with the local herring abundance in Jade Bay (this abundance was termed A-JB-H), close to the common tern colony. We used a ranking approach to address the overall food abundance per year (covering the two age groups of herring as well as the sprat stock). A combination of two or three abundance indices may be the most suitable approach to explain the annual variability in the hormone data. We therefore ranked the three fish abundance measures (herring 0: H0, herring 1: H1, and sprat: S) for the North Sea for all analyzed years (2006–2012) in ascending order (worst to best year). This was then used to calculate the mean rank for every combination of two or three abundance measures (H01, H0S, H1S, and H01S; the ranked indices were termed r-NS-H01, r-NS-H0S, r-NS-H1S, and r-NS-H01S, respectively). Fish abundance indices as well as fish rank indices in the North Sea were positively, but not significantly, correlated with herring abundance in Jade Bay (see Online Resource 2 in the ESM).

To determine the most suitable food abundance parameter for explaining the baseline prolactin and corticosterone levels, a general linear mixed model was fitted with prolactin or corticosterone concentration as response variable, and then step by step with the abundance indices as well as fish ranks as fixed factors. The model that best explained both hormone concentrations was found to include the fish ranks H01 and H0S (see Online Resource 3 in the ESM). These ranks were used for the full model that analyzed hormone levels. Another argument for using the fish ranks instead of abundance indices was provided by the relations with baseline prolactin and corticosterone; the correlations between both hormones and fish ranks were stronger overall than those with abundance indices, though not significant in all cases (see Online Resource 4 in the ESM).
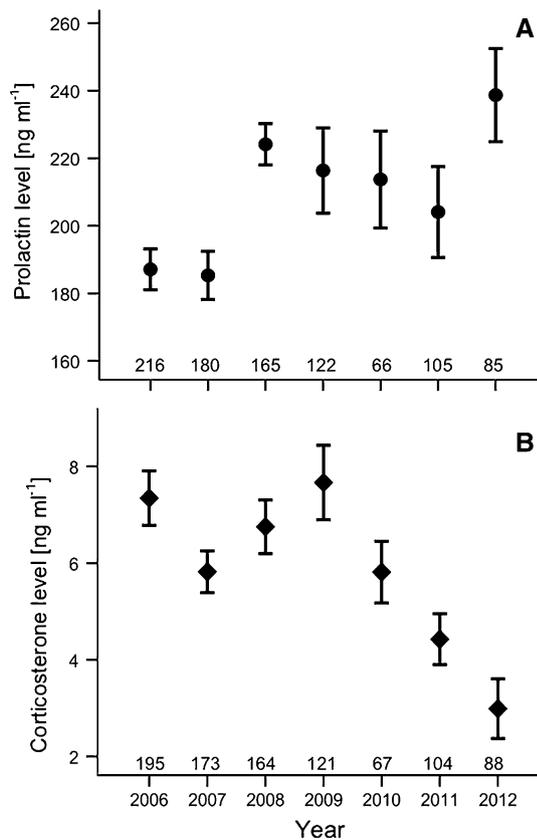
**Fig. 1** Mean ± 95 % CI for baseline prolactin (**a**) and corticosterone (**b**) levels in common terns from 2006 to 2012. If the confidence intervals overlap, the levels were significantly different between years. The sample size $N$ is shown just above the $x$-axis in each plot

Using a generalized linear model (GEE) with a binary distribution and a logit link function, we tried to predict the occurrence of (1) at least one hatchling or not, (2) at least one fledgling or not, and (3) at least one fledged chick per pair. Baseline prolactin, corticosterone, fish abundance/fish ranks, year, bird ID, and their two-way interactions were included as independent variables. Id code was introduced

as a subject and sample as a repeated measure. We then used a stepwise backwards elimination approach to exclude nonsignificant terns until only significant ($P < 0.05$) parameters remained in the model. The analysis was done separately for males and females, as we often sampled both pair mates and had to avoid pseudoreplication of breeding success parameters (which are a function of both pair members).

## Results

Year effect on hormones and reproductive parameters

Baseline prolactin and corticosterone levels were significantly different between years (prolactin: $\chi^2 = 173.044$, $P < 0.001$, $N = 939$; corticosterone: $\chi^2 = 199.148$, $P < 0.001$, $N = 912$). Mean baseline prolactin measured during 2006 and 2007 was significantly lower than it was during 2008–2012 (Fig. 1a). Furthermore, the mean concentration measured in 2008 was significantly higher than in 2011, and the mean level measured in 2012 was the highest overall (Fig. 1a). Mean baseline corticosterone level measured in 2011 was significantly lower than that between 2006 and 2010, and the mean concentration in 2012 was the lowest overall (Fig. 1b). Furthermore, the mean titer in 2006 and 2009 was significantly higher than it was in 2007 and 2010 (Fig. 1b). Annual mean baseline prolactin and corticosterone levels in the population were not significantly correlated with each other ($r = -0.351$, $P = 0.440$, $N = 7$).

Hatching, fledging, and breeding success (fledglings per pair) were also different between years (hatching success: $P < 0.001$, $\chi^2 = 25.401$, $N = 734$; fledging success: $P < 0.001$, $\chi^2 = 82.497$, $N = 734$; breeding success: $P < 0.001$, $\chi^2 = 77.436$, $N = 734$; Table 1). Mean hatching success was higher in 2008 and 2011 than in all other years except for 2012 (Table 1), with the other years showing

**Table 1** Mean hatching success (proportion of all eggs laid from which chicks hatched), fledging success (proportion of hatchlings that became fledglings) and number of fledged chicks per pair in each analyzed year

| Year | Hatching success | Fledging success | Number of fledglings | $N$ |
|------|------------------|------------------|----------------------|-----|
| 2006 | $0.76 \pm 0.33^{08}$ | $0.40 \pm 0.36^{09-12}$ | $0.66 \pm 0.63^{09-12}$ | 167 |
| 2007 | $0.68 \pm 0.37^{08,11,2}$ | $0.38 \pm 0.40^{09-12}$ | $0.54 \pm 0.65^{08-12}$ | 132 |
| 2008 | $0.86 \pm 0.25^{06-10}$ | $0.34 \pm 0.30^{09-12}$ | $0.70 \pm 0.63^{07,09,10,12}$ | 128 |
| 2009 | $0.70 \pm 0.35^{08,11,12}$ | $0.21 \pm 0.27^{06-12}$ | $0.31 \pm 0.47^{06-12}$ | 99 |
| 2010 | $0.70 \pm 0.38^{08}$ | $0.60 \pm 0.42^{06-09}$ | $1.15 \pm 0.99^{06-09}$ | 55 |
| 2011 | $0.84 \pm 0.27^{06,07,09,l0}$ | $0.58 \pm 0.40^{06-09}$ | $0.92 \pm 0.89^{06-09,12}$ | 85 |
| 2012 | $0.85 \pm 0.24^{07,09}$ | $0.59 \pm 0.34^{06-09}$ | $1.25 \pm 0.80^{06-09,11}$ | 68 |

Superscript numbers indicate significant differences between the years indicated ($P < 0.05$). Sample size $N$ (nests) is shown for each year in the last column

**Table 2** Outcome of the GLM that analyzed baseline prolactin (a) and corticosterone (b) levels in common terns in relation to sex, ranked fish abundance in the North Sea (r-NS-H01/H0S/H1S), nest, ID, and year

| Variables in the model | AIC | $\Delta$AIC | $W_i$ |
|---|---|---|---|
| (a) Prolactin | | | |
| r-NS-H01, r-NS-H0S, r-NS-H01 × r-NS-H0S, sex × r-NS-H01, sex × r-NS-H0S | 10,150.322 | 0 | 0.183 |
| r-NS-H01, r-NS-H0S, nest, r-NS-H01 × r-NS-H0S, sex × r-NS-H01, sex × r-NS-H0S | 10,150.492 | 0.170 | 0.168 |
| r-NS-H01, r-NS-H0S, sex, ID, r-NS-H01 × r-NS-H0S, sex × r-NS-H01, sex × r-NS-H0S | 10,151.198 | 0.876 | 0.118 |
| ID, r-NS-H01 × r-NS-H0S, sex × r-NS-H01 | 10,158.280 | 0.958 | 0.113 |
| r-NS-H01, r-NS-H0S, year, r-NS-H01 × r-NS-H0S, sex × r-NS-H01, sex × r-NS-H0S | 10,151.329 | 1.007 | 0.111 |
| r-NS-H01, r-NS-H0S, sex, ID, nest, r-NS-H01 × r-NS-H0S, sex × r-NS-H01, sex × r-NS-H0S | 10,151.907 | 1.585 | 0.083 |
| r-NS-H01, r-NS-H0S, sex, year, nest, r-NS-H01 × r-NS-H0S, sex × r-NS-H01, sex × r-NS-H0S | 10,152.009 | 1.687 | 0.079 |
| ID, nest, r-NS-H01 × r-NS-H0S, sex × r-NS-H01 | 10,152.260 | 1.938 | 0.069 |
| (b) Corticosterone | | | |
| r-NS-H01, r-NS-H0S, sex, year, r-NS-H01 × r-NS-H0S | 1,248.411 | 0 | 0.207 |
| year, ID, r-NS-H01 × r-NS-H0S, r-NS-H0S × sex | 1,248.682 | 0.271 | 0.181 |
| year, ID, nest, r-NS-H01 × r-NS-H0S, r-NS-H0S × sex | 1,248.682 | 0.271 | 0.181 |
| year, ID, r-NS-H01 × r-NS-H0S, r-NS-H01 × sex | 1,248.812 | 0.401 | 0.169 |
| year, r-NS-H01 × r-NS-H0S, r-NS-H0S × sex | 1,249.188 | 0.777 | 0.140 |
| year, ID, nest, r-NS-H01 × r-NS-H0S, r-NS-H01 × sex | 1,250.812 | 2.401 | 0.062 |
| year, r-NS-H01 × r-NS-HOS, r-NS-H01 × sex | 1,250.916 | 2.505 | 0.059 |

r-NS-H01/H0S/H1S is the ranked fish abundance obtained by ranking abundance measures of herring (age classes 0 and 1) and sprat and calculating the mean rank of two combined indices.

We have shown all models with $\Delta$AIC < 4 because they are supported by the data. AIC, $\Delta$AIC, and Akaike's weight $W_i$ are all presented

similar levels of hatching success. However, fledging success was highest during the last three years (2010–2012), and the mean concentration in 2009 was significantly lower than it was in all other years (Table 1). The same was true of breeding success (Table 1). Hatching success was not significantly related to fledging or breeding success during each year of the study ($r < 0.5$, $P > 0.3$, $N = 7$, respectively), whereas fledging and breeding success were significantly positively correlated ($r = 0.939$, $P = 0.002$, $N = 7$).

Food abundance and hormone concentration

The procedure for selecting models including ranked fish abundance (herring and sprat indices) within the North Sea (r-NS-H01, r-NS-H1S, r-NS-H0S) indicated that the model containing different fish ranks and their interaction with sex was the best model for explaining prolactin levels in common terns (Table 2a). However, the variance in the prolactin concentration explained by the fish ranks was generally low (H01: 4.1 %, H0S: 4.6 %, H01 × H0S: 1 %, H01 × sex: 2.3 %, H0S × sex: 2.5 %). Individual corticosterone level was best expressed by a model containing fish ranks, their interaction, sex, and year (Table 2b). The variance in the corticosterone data explained by the abovementioned parameters was again quite low (H01: 1.5 %, H0S: 1.6 %, H01 × H0S: 2.2 %, sex: 2.5 %, year: 3.6 %).

**Table 3** Outcome of the GLM that analyzed baseline prolactin (a) and corticosterone (b) levels in common terns in relation to sex, herring abundance in Jade Bay (A-JB-H), nest, ID, and year

| Variables in the model | AIC | $\Delta$AIC | $W_i$ |
|---|---|---|---|
| (a) Prolactin | | | |
| A-JB-H, sex, nest, A-JB-h × sex | 10,078.330 | 0 | 0.187 |
| sex, A-JB-H × sex | 10,078.935 | 0.605 | 0.135 |
| A-JB-H, A-JB-h × sex | 10,078.935 | 0.605 | 0.135 |
| A-JB-H, sex, A-JB-h × sex | 10,078.935 | 0.605 | 0.135 |
| A-JB-H, sex, ID, A-JB-h × sex | 10,079.775 | 1.445 | 0.090 |
| A-JB-H, sex, ID, nest, A-JB-h × sex | 10,079.842 | 1.512 | 0.088 |
| A-JB-H, sex, year, A-JB-h × sex | 10,079.901 | 1.571 | 0.085 |
| A-JB-H, sex, year, nest, A-JB-h × sex | 10,079.930 | 1.600 | 0.084 |
| A-JB-H, sex, year, ID, A-JB-h × sex | 10,081.901 | 3.571 | 0.031 |
| A-JB-H, sex, year, ID, nest, A-JB-h × sex | 10,081.930 | 3.600 | 0.031 |
| (b) Corticosterone | | | |
| A-JB-H, sex, ID | 1,232.309 | 0 | 0.407 |
| A-JB-H, sex, ID, nest | 1,234.309 | 2.000 | 0.150 |
| A-JB-H, sex | 1,234.458 | 2.149 | 0.139 |
| A-JB-H, sex, ID, year | 1,234.720 | 2.411 | 0.122 |
| A-JB-H, sex, year | 1,236.286 | 3.977 | 0.056 |

A-JB-H refers to the number of herring per 10,000 m³ of water in Jade Bay.

We have shown all models with $\Delta$AIC < 4 because they are supported by the data. AIC, $\Delta$AIC, and Akaike's weight $W_i$ are presented

The procedure for selecting models including local herring abundance in Jade Bay (A-JB-H) revealed that the best model for explaining prolactin levels in common terns included herring abundance, sex, nest, and herring × sex (Table 3a). Between 1 and 9 % of the variance was explained (herring 9.1 %, sex 1 %, nest 1.4 %, herring × sex 4.1 %). In years with higher herring abundances, terns exhibited higher prolactin levels overall (Fig. 2). In the case of corticosterone, the best model was found to include herring, sex, and the bird's ID (Table 3b), with a low level of explained variance in the corticosterone data overall (herring: 12.1 %, sex: 2.5 %, ID: 1.4 %). In contrast to prolactin, lower corticosterone levels were generally observed in years with higher herring abundances (Fig. 3).

Reproductive success and hormone concentration

*Colony means*

Mean hatching, fledging, and breeding success in the colony was not significantly related to mean prolactin level during the years of the study (hatching success: $r_s = 0.495$, $P = 0.259$; fledging success: $r_s = 0.165$, $P = 0.724$; breeding success: $r_s = 0.454$, $P = 0.306$, $N = 7$, respectively); nor was baseline corticosterone related to hatching success ($r_s = -0.472$, $P = 0.285$). However, fledging and breeding success were significantly negatively related to corticosterone level (fledging success: $r_s = -0.800$, $P = 0.031$; breeding success: $r_s = -0.781$, $P = 0.038$, $N = 7$, respectively).

Intra-individual and intra-pair relationships

In females that were sampled repeatedly in successive years, an increase in baseline prolactin from the second year to the third and from the third to the fourth year was significantly positively linked to an increase in hatching success (2nd year to 3rd year: $r = 0.280$, $P = 0.039$, $N = 55$; 3rd year to 4th year: $r = 0.367$, $P = 0.030$, $N = 35$). However, we did not find a significant correlation for the other years ($-0.3 < r < 0.6$, $P > 0.1$ in all cases, $7 < N < 104$). Males, on the other hand, showed no significant relationship between hormones and success parameters in subsequent years ($-0.5 < r < 0.5$, $P > 0.1$, $5 < N < 101$). Baseline prolactin and corticosterone levels were significantly positively correlated between pair mates (prolactin: $r = 0.180$, $P = 0.009$, $N = 211$; corticosterone: $r_s = 0.308$, $P < 0.001$, $N = 200$).

Hormone concentrations as predictors for reproductive success

We found a significantly positive correlation between prolactin level and fledging success (2008: $r_s = 0.328$, $P = 0.002$, $N = 85$; 2011: $r_s = 0.398$, $P = 0.002$, $N = 57$)
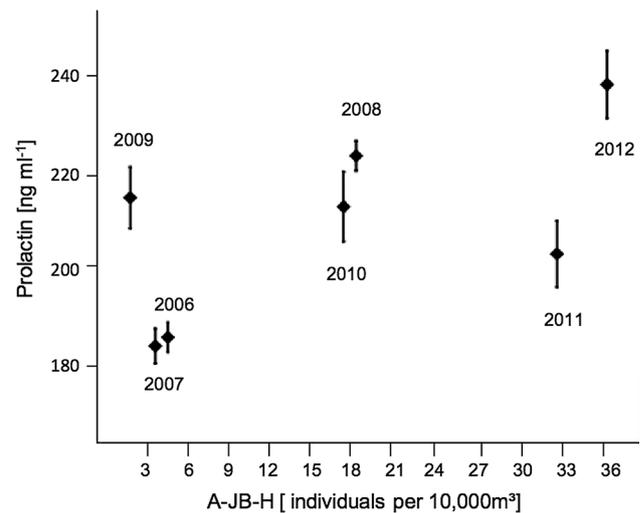


**Fig. 2** Mean baseline prolactin concentration (ng/ml$^{-1}$) $\pm$ 1 SE in relation to herring abundance (A-JB-H) in Jade Bay (individuals per 10,000 m$^3$) during the years 2006–2012
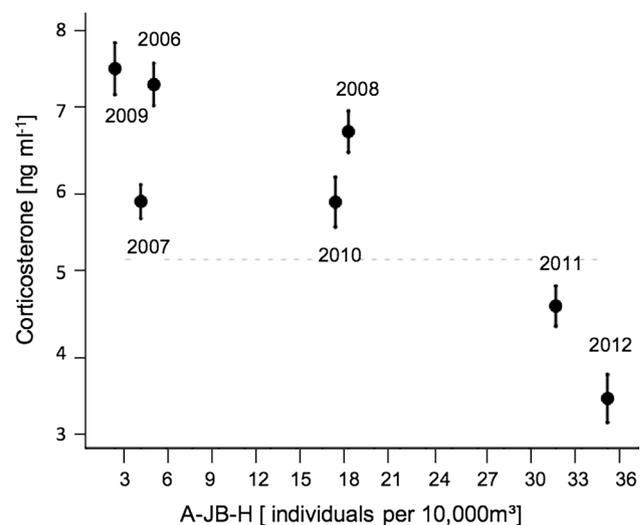


**Fig. 3** Mean baseline corticosterone concentration (ng/ml$^{-1}$) $\pm$1 SE in relation to herring abundance (A-JB-H) in the Jade Bay (individuals per 10,000 m$^3$) during the years 2006–2012

as well as breeding success (2008: $r_s = 0.295$, $P = 0.006$, $N = 85$; 2011: $r_s = 0.295$, $P = 0.026$, $N = 57$) in females in 2008 and 2011. In males, hatching success and baseline prolactin level were significantly positively linked in 2006 ($r_s = 0.267$, $P = 0.006$, $N = 105$), as were fledging and breeding success with corticosterone titer in 2009 (fledging success: $r_s = 0.253$, $P = 0.043$; breeding success: $r_s = 0.250$, $P = 0.047$, $N = 64$, respectively). Additionally, we observed a significantly positive correlation between fledging success and prolactin level in 2012 ($r = 0.328$, $P = 0.039$, $N = 40$). Hormone levels and success

**Table 4** Outcome of the GEE that analyzed hatching, fledging, and breeding success (the occurrence of at least one hatchling/fledgling/surviving fledgling, respectively) for males (a) and females (b) in relation to hormone levels, ranked fish abundance in the North Sea (r-NS-H01/H0S/H1S), year, and ID

| Analyzed parameter | Explanatory variable | Wald $\chi^2$ | df | P |
|---|---|---|---|---|
| **(a) Males** | | | | |
| Hatching success | Prolactin | 8.513 | 1 | 0.004 |
| Fledging success | r-NS-H01 | 5.723 | 1 | 0.017 |
| | r-NS-H0S | 4.484 | 1 | 0.034 |
| | Year | 3.855 | 1 | 0.049 |
| | r-NS-H01 × year | 5.715 | 1 | 0.017 |
| | r-NS-H0S × year | 4.470 | 1 | 0.035 |
| Breeding success | Year | 4.910 | 1 | 0.027 |
| | r-NS-H01 | 15.990 | 1 | <0.001 |
| | r-NS-H0S | 14.308 | 1 | <0.001 |
| | r-NS-H01 × year | 15.973 | 1 | <0.001 |
| | r-NS-H0S × year | 14.278 | 1 | <0.001 |
| | r-NS-H01 × corticosterone | 5.288 | 1 | 0.021 |
| | r-NS-H0S × corticosterone | 6.458 | 1 | 0.011 |
| **(b) Females** | | | | |
| Hatching success | Prolactin | 23.357 | 1 | <0.001 |
| Fledging success | r-NS-H01 | 7.378 | 1 | 0.007 |
| | r-NS-H0S | 6.177 | 1 | 0.013 |
| | r-NS-H01 × year | 7.373 | 1 | 0.007 |
| | r-NS-H0S × year | 6.167 | 1 | 0.013 |
| Breeding success | r-NS-H01 | 12.362 | 1 | <0.001 |
| | r-NS-H0S | 11.367 | 1 | 0.001 |
| | r-NS-H01 × year | 12.354 | 1 | <0.001 |
| | r-NS-H0S × year | 11.355 | 1 | 0.001 |

r-NS-H01/H0S/H1S refer to the ranked fish abundance obtained by ranking herring and sprat abundances (A-NS-H0/H1/S) and then calculating the mean rank of two combined indices.

We present the last step of the model after stepwise exclusion of insignificant parameters and interaction terms

**Table 5** Outcome of the GEE that analyzes hatching, fledging, and breeding success (the occurrence of at least one hatchling/fledgling/surviving fledgling, respectively) for males (a) and females (b) in relation to hormone values, herring abundance in Jade Bay (A-JB-H), year, and ID

| Analyzed parameter | Explanatory variable | Wald $\chi^2$ | df | P |
|---|---|---|---|---|
| **(a) Males** | | | | |
| Hatching success | Prolactin | 8.513 | 1 | 0.004 |
| Fledging success | Corticosterone | 8.139 | 1 | 0.004 |
| | A-JB-H | 10.874 | 1 | 0.001 |
| Breeding success | Corticosterone | 6.481 | 1 | 0.011 |
| | A-JB-H | 16.210 | 1 | <0.001 |
| | Year | 4.811 | 1 | 0.049 |
| **(b) Females** | | | | |
| Hatching success | Prolactin | 17.352 | 1 | <0.001 |
| | A-JB-H | 7.075 | 1 | 0.008 |
| | Corticosterone | 5.753 | 1 | 0.016 |
| Fledging success | A-JB-H | 9.088 | 1 | 0.003 |
| | Year × corticosterone | 3.886 | 1 | 0.049 |
| | Year | 4.585 | 1 | 0.043 |
| Breeding success | Year | 6.331 | 1 | 0.012 |

A-JB-H refers to herring abundance (number of individuals per 10,000 m$^3$ water) in Jade Bay

We present the last step of the model after stepwise exclusion of insignificant parameters and interaction terms

Jade Bay) best predicted fledging and breeding success (Tables 4, 5). In females, the best model contained fish abundance and year using North Sea or Jade Bay data (Tables 4, 5). Parents with an increased baseline corticosterone level were more likely to produce a fledgling (Fig. 5).

## Discussion

We found clear evidence for strong annual differences in hormone levels as well as correlations between hormone levels and parameters of reproductive success. However, the connection between hormones and success was year and sex dependent. We detected an overall positive effect of high prolactin and elevated corticosterone baseline concentrations on reproductive success in common terns.

### Year effect

All of the analyzed reproductive success parameters were significantly different between years, with 2010–2012 being the most successful ones during our study period. The year effect increased from hatching to fledging success, and was most pronounced in the number of fledged chicks per pair. In most studies, weather conditions and
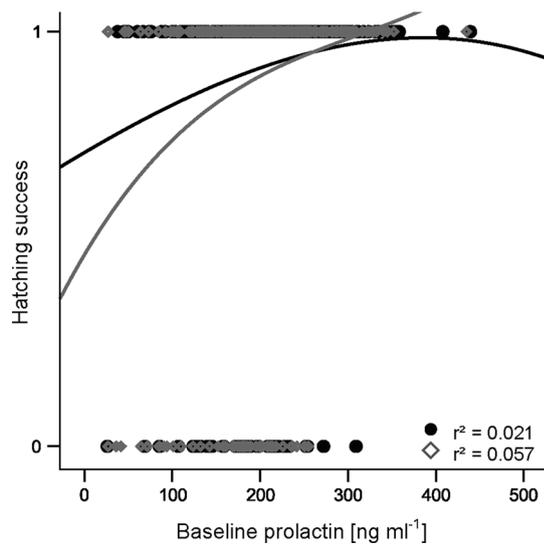
parameters were not significantly linked to each other in either sex in any other year ($-0.2 < r < 0.3$, $P > 0.1$, $14 < N < 106$).

To predict reproductive success, we used hormone concentrations, fish abundance (r-NS-H01, H0S, H1S, or A-JB-H), ID of birds, and year as independent variables. In both models (including ranked fish abundance in the North Sea or herring abundance in the Jade Bay), prolactin baseline level was significantly correlated with hatching success in both sexes (Tables 4, 5). Males and females with higher prolactin titers were more likely to produce a hatchling (Fig. 4).

In males, baseline corticosterone concentration, year of sampling, and fish abundance (in the North Sea or

**Fig. 4** Baseline prolactin concentration (ng/ml$^{-1}$) in relation to hatching success (*0* no hatchling, *1* at least one hatchling) for males (*black circles*) and females (*open gray squares*). Cubic curves (*black* males, *gray* females) showed the best fit to the data. $r^2$ for both sexes in the *lower right corner*. Note that *black dots* are not always visible through *gray squares*
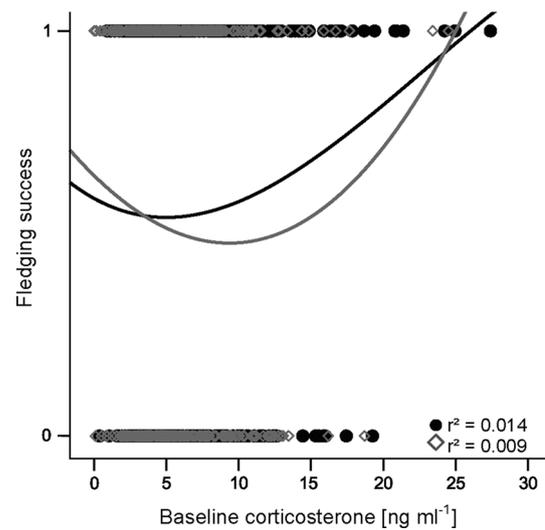
**Fig. 5** Baseline corticosterone concentration (ng/ml$^{-1}$) in relation to fledging success (*0* no fledgling, *1* at least one fledgling) for males (*black dots* males, *gray* females) and females (*open gray squares*). Cubic curves (*black* males, *gray* females) showed the best fit to the data. $r^2$ for both sexes in the lower right corner. Note that *black dots* are not always visible through *gray squares*

especially food abundance drive the differences in breeding success between years (Becker 1998; Quillfeldt 2001; Golet et al. 2004). Therefore, a food shortage should have the most severe consequences on the number of fledged chicks, as parents are most dependent on a high food supply during the nestling phase. We know that the abundances of herring and sprat, one of the most important food sources of common terns in the North Sea, varied between our study years (Dänhardt and Becker 2011a). At the population level, high food abundance was linked to increased prolactin concentration and decreased corticosterone concentration. Food abundance is one factor that leads to differences in the reproductive success of terns (Dänhardt and Becker 2011a). Another parameter that affects breeding success is age or experience of birds: Limmer and Becker (2010) and Rebke et al. (2010) demonstrated increasing reproductive success with enhanced breeding experience at both the population and individual levels. However, as breeding experience is linked to hormone levels in common terns (Riechert et al. 2012), separating the effects of experience and hormone concentrations is a difficult task, so we did not include experience in our analyses.

Hormone levels also differed considerably between years: baseline prolactin titer was low during 2006 and 2007 and much higher in all other years of the study. Corticosterone concentration, on the other hand, was highest in 2006 and 2009 and lowest in 2012. Both hormones are known to vary between years (Delehanty et al. 1997; Romero and Wikelski 2001; Lanctot et al. 2003; Kitaysky

et al. 2007; Welcker et al. 2009). Romero et al. (2000) found evidence that various weather parameters affect baseline corticosterone in different bird species, and corticosterone level was found to be higher in marine iguanas (*Amblyrhunchus cristatus*) during the year with an El Niño event (Romero and Wikelski 2001). Likewise, prolactin was affected by weather conditions in Wilson's phalaropes (*Phalaropus tricolour*), with a prolonged draught leading to decreased prolactin levels (Delehanty et al. 1997). However, we suggest that the direct effect of weather conditions on hormone titers may not be as strong as the indirect effect of weather on food abundance.

Some authors suggest that baseline corticosterone may be used as an indicator of food availability at both the individual and population levels (Kitaysky et al. 1999, 2007; Angelier et al. 2007a; Buck et al. 2007; Doody et al. 2008), with high titers indicating low food abundance and poor body condition (Kitaysky et al. 2007, 2010; Welcker et al. 2009). We also found a lower corticosterone concentration in years with higher herring abundances in Jade Bay or North Sea. Prolactin, on the other hand, decreases with ongoing fasting/low food supply and worsening body mass of adults (Criscuolo et al. 2003; O'Dwyer et al. 2006; Riechert et al. 2014). Accordingly, in years with higher herring abundances, and probably birds in better body condition, common terns exhibited increased prolactin titers. Exceptions were the years 2009 and 2011: in 2009, the prolactin titer was quite high but herring abundance was low. An explanation could be greater availability of other

important prey species for common terns, such as smelt (*Osmerus eperlanus*), anchovies (*Engraulis encrasicolus*), or flatfish (*Plattichthys flesus*), which could perhaps compensate for a low herring abundance (e.g., Wendeln 1997). From previous years, it is known that common terns can also forage in freshwater if marine prey is not abundant (e.g., Becker et al. 1987; Wendeln 1997). In 2011, on the other hand, herring was highly abundant in foraging areas near the colony, but the mean prolactin concentration was rather low. We suggest that harsh weather conditions such as storms during the breeding period posed a challenge for common terns during foraging, leading to decreased prolactin despite a high food abundance. Moreover, high temperatures may result in migration of fish below the surface of the water, where common terns cannot catch them as they can only dive 0.5 m below the surface (Dänhardt and Becker 2011b). Indeed, the wind speed was quite high during several days of incubation, and the mean temperature during May and June was elevated compared to other years (source: http://wetter.online.de, region of Wilhelmshaven), as was the mean water temperature (Dänhardt 2013). Finally, Riechert et al. (2012) found low repeatability of individual hormone concentrations in common terns between years, suggesting that, even at the individual level, differences between years in weather or food abundance may drive variations in hormone levels.

Hormone concentrations and reproductive success

One very important factor that influences breeding success in seabirds is food availability (Golet et al. 2004; Dänhardt and Becker 2011a). Accordingly, we found a strong effect of prey abundance on fledging and breeding success in common terns. Hatching success, on the other hand, was less dependent on food abundance, which could be explained by the lower energy constraints on parents during incubation (Riechert et al. 2014).

As difficult foraging conditions are normally linked with a low overall breeding success, high baseline corticosterone could be an indicator of low breeding success; this relationship is termed the cort-fitness hypothesis (Bonier et al. 2009a). Accordingly, we found a negative connection between colony means of fledging success and baseline corticosterone in our data. In kittiwakes (*Rissa tridactyla*), on the other hand, Lanctot et al. (2003) did not detect a relationship between baseline corticosterone and food availability during the incubation phase, whereas Kitaysky et al. (2007) found such a relationship during the chick-rearing phase in the same species. However, a review of the cort-fitness hypothesis by Bonier et al. (2009a) indicated that the predicted negative relationship between corticosterone and fitness was found in only half of the studies included, whereas the other studies detected no relationship or even

a positive one. Corticosterone levels are quite plastic and vary with the season (Angelier et al. 2007a). This could be one reason why one measurement per individual and season may not be sufficient to detect a relationship between reproductive success and corticosterone level. Additionally, the relationship between corticosterone and fitness is not static; it can vary over time and with sex and reproductive strategy (Bonier et al. 2009b; Jaatinen et al. 2013).

The mean breeding success was quite low during most of our study years (Szostek and Becker 2012). However, common terns seem to be able to buffer low success and probably low food abundance without experiencing a considerable increase in baseline corticosterone. Furthermore, some study years were characterized by high food abundance, leading to high levels of hatching success and chick growth, but some stormy days during the nestling phase resulted in high chick mortality and therefore low reproductive success (unpublished data). This illustrates that hormone levels measured during incubation are not necessarily tightly linked to later hatching success, and even less so to fledging or breeding success.

Nevertheless, we found a significant and positive relationship between hatching or fledging success and baseline hormone levels during some of the years of the study. In contrast, Jaatinen et al. (2013) found a negative relationship between baseline corticosterone level and the probability of at least one hatchling, though they also revealed a slightly increased corticosterone titer in late-laying females that expend more energy. In common terns, the levels of both hormones were good predictors of reproductive success: high prolactin concentrations were linked to a higher hatching success in both sexes, and increased fledging and breeding success were linked to elevated baseline corticosterone in males. In females, fledging success was best explained by prey abundance and year—factors that were also significant in males. There seems to be a long-lasting effect of the hormone concentration during incubation on hatching and fledging success some weeks later. However, our study could not clarify whether there is a direct and causal connection between hormone values and reproductive success or rather if these parameters are linked with another factor like quality of birds. But results so far provide promising avenues for future (experimental) work.

The overall breeding success of house sparrows (*Passer domesticus*) was also linked to a high prolactin level (Ouyang et al. 2011). In our study, baseline prolactin could be used as a predictor of hatching success in both sexes, with higher prolactin levels found in birds with more hatchlings. Prolactin is associated with constant incubation behavior (Wang and Buntin 1999), which prevents eggs from getting cold or predated and ultimately leads to greater hatching success. Accordingly, Angelier et al. (2013) found a positive relationship between baseline prolactin and hatching

success in free-living Cape petrels (*Daption capense*). Furthermore, reduced prolactin was associated with decreased nest attendance and lower breeding success (Angelier et al. 2009; Spee et al. 2010). During some of the years of our study, a higher prolactin level was also associated with more fledglings. This may be due to the positive influence of elevated prolactin on the feeding rate of young (Buntin 1996; Duckworth et al. 2003; Ouyang et al. 2011). Moreover, prolactin stimulates the brooding and guarding of young in ring doves (Wang and Buntin 1999), adding to the increased success achieved by reducing predation risk.

Just as in our study, a greater number of chicks was positively linked to higher baseline corticosterone in female tree swallows (*Tachycineta bicolour*, Bonier et al. 2009b, 2013). In house sparrows, individuals with increased corticosterone levels during breeding also fledged more young (Ouyang et al. 2011). In contrast, many other studies found evidence for a negative relationship between corticosterone and overall productivity (Buck et al. 2007; Kitaysky et al. 2007, 2010; Angelier et al. 2010; Satterthwaite et al. 2012). A long-term or really strong increase in corticosterone up to stress levels leads to nest abandonment (Spee et al. 2010). Accordingly, Angelier et al. (2009) found low reproductive success in kittiwakes after corticosterone implantation, which resulted in a two-day increase in stress level. A slightly increased baseline corticosterone level is, however, known to raise activity levels (Astheimer et al. 1992; Angelier et al. 2007a), increase time and effort during foraging (Angelier et al. 2007b), and facilitate energy (McEwen and Wingfield 2003). This is in line with the results of an experiment by Crossin et al. (2012) in the macaroni penguin (*Eudyptes chrysolophus*), where a corticosterone implant led to a higher baseline level, resulting in increased diving activity and improved breeding success. Finally, an increase in corticosterone level in kittiwakes could be associated with elevated energy stores due to foraging if the energetic load is low (Shultner et al. 2013a). Consequently, common tern fathers with higher plasma corticosterone levels may be more active foragers, ultimately leading to higher fledging success. In mothers, which start feeding their chicks later, baseline corticosterone was not as useful for predicting fledging success as it was in fathers. Furthermore, Doody et al. (2008) showed a greater feeding rate and increased chick growth in common murres (*Uria aalge*) with higher corticosterone concentrations, and tree swallow females with increased corticosterone titers during the nestling phase had faster-growing chicks (Bonier et al. 2009b) and provisioned them at a higher rate (Bonier et al. 2013). Additionally, chick mass in macaroni penguins was positively correlated with the baseline corticosterone levels of the parents (Crossin et al. 2012). Finally, elevated corticosterone in kittiwakes breeding in the Atlantic resulted in increased chick growth

and higher reproductive success of parents (Shultner et al. 2013b).

In males, increased corticosterone concentration during incubation could support active exploration of foraging grounds prior to hatching (Becker et al. 1993). This positive relationship between corticosterone and fitness is summarized in the cort-adaptation hypothesis (Bonier et al. 2009b), which suggests that elevated corticosterone supports a higher allocation of resources to reproduction and thereby an increased reproductive output. Recently, a new hypothesis was developed from the cort-adaptation hypothesis by Bonier et al. (2013): the context-dependent hypothesis. It claims that elevated corticosterone only promotes allocation of resources to reproduction when the current value of reproduction is high.

But why did we find negative correlations between colony means of baseline corticosterone and fledging and breeding success, whereas these parameters were positively correlated within individuals? We suggest that colony means of hormones reflect overall year effects, with low corticosterone levels indicating good foraging conditions (Kitaysky et al. 2007, 2010; Doody et al. 2008), leading to relatively low foraging efforts of individuals. Accordingly, Shultner et al. (2013a) found low corticosterone concentrations in kittiwakes that received supplementary feeding. In line with this, we observed lower mean corticosterone levels in years with higher herring abundances. On the other hand, increased investment and rearing effort led to a raised baseline corticosterone titer (Bonier et al. 2009b; Crossin et al. 2012). Therefore, even during good years with a low mean corticosterone level overall, some individuals expend more effort and energy (expressed as an increased baseline corticosterone concentration) than others, and ultimately exhibit greater reproductive success. However, the question of why hormone concentrations were related to only some of the success parameters, and only in some years, remains. Satterthwaite et al. (2012) also analyzed different environmental parameters in relation to success and corticosterone level, and concluded that—despite the presence of weak correlations—multiple factors could exert competing effects and vary between locations and years. Therefore, to answer the question we need further studies that analyze fine-scale food abundance in different periods (incubation, chick-rearing phase) in relation to hormone levels measured in the same period.

## Conclusions

Baseline hormone concentrations and parameters of reproductive success were dependent on the year, illustrating the influence of environmental conditions such as food abundance or weather. We showed that baseline prolactin and corticosterone were positively linked to reproductive success in

common terns. However, this correlation was not consistent across years, possibly due to the time interval between sampling and hatching or fledging and inter-individual differences in coping with stressful events such as food shortages. However, high prolactin could support reproductive success by enhancing incubation or chick guarding or increasing the feeding rate. Slightly elevated baseline corticosterone, on the other hand, may increase foraging activity, feeding performance, and feeding rate of young. At the population level, food abundance was negatively linked to corticosterone level and positively related to prolactin titer, reflecting the overall foraging conditions for common terns.

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