

Why do experienced birds reproduce better? Possible endocrine mechanisms in a long-lived seabird, the common tern

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ABSTRACT

The influence of age or breeding experience on reproductive success in vertebrates is well known but physiological mechanisms came into focus just recently. Assessing hormone levels could allow insights into these mechanisms and reproductive strategies in long-lived species. Prolactin and corticosterone are two hormones involved in breeding decisions: high prolactin values are necessary for expressing breeding behavior whereas corticosterone is related to activity or stress. We analyzed baseline prolactin and corticosterone under field conditions in common terns (*Sterna hirundo*) between 2006 and 2010. We took 760 blood samples of 346 known birds 9–14 days after their clutch completion, obtained via blood-sucking bugs (*Dipetalogaster maximus*), a non-invasive method with negligible stress for the birds. Many individuals were sampled repeatedly during the study period allowing investigation of hormone change on individual level. Prolactin levels increased during the early breeding career, which was confirmed on individual level, whereas corticosterone levels increased mostly in experienced birds, more pronounced in males. Low hormone levels during the first years of breeding could indicate a reduced ability of the endocrine system to secrete hormones or it might express a down-regulation to limit parental expenditure. Higher corticosterone values of males could be related to increased foraging activity. Amongst the oldest birds, prolactin seemed to increase in males but not in females. This possible consequence of female senescence might be compensated by high values of male mates. Body mass showed only a weak positive correlation with prolactin level and no correlation with corticosterone concentration.

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1. Introduction

Many studies described an age-related change in reproductive performance in long-lived vertebrates: generally young breeders show an increase in breeding success over the first reproductive attempts [22,33,43,52,65]. However, a higher breeding experience, which is tightly linked to older age e.g. [34,52], was shown to be more important for a good success than age per se [4,21,52]. After a stabilization of breeding success on a high level in middle-aged birds some studies found a decrease in the oldest individuals [13,17,31,65] possibly related to senescence, which is a loss of physiological functions leading to a reduced reproduction or chance to survive [44]. Another possibility could be a selection of phenotypes displaying low reproductive effort [33].

In order to gain more knowledge about individual reproductive strategies or the consequences of the age/experience structure of a population, it is crucial to understand how experience-related changes in reproductive success are physiologically mediated. One approach, which allows insights into mechanisms and repro-

ductive strategies, is to study hormone levels because of their involvement in breeding decisions. One hormone important for reproductive behavior in birds is corticosterone, the main avian glucocorticoid. Corticosterone levels rise within a few minutes after exposure to stress [68]. A moderate short term elevation of glucocorticoids can have positive effects: It could enhance foraging activity [5] and survival via the stimulation of gluconeogenesis, or escape behavior [72,83]. More precisely, glucocorticoids inhibit glucose uptake into tissues resulting in an increase in the free fraction [67] what supports an animal in coping with stressful situations or in recovering from a stressful event. During the breeding phase a slightly increased baseline level could be linked with a higher parental effort and feeding of young [46,62]. On the other hand a high circulating corticosterone level ('stress level') maintained over a longer period indicates stress and inhibits parental behavior [83]. Owing to the role of corticosterone during breeding and to contradicting studies on the link of baseline corticosterone level and breeding experience [2–4,38], it is worth to further investigate the relationship between experience and breeding decisions or reproductive expenditure [75].

For an adequate breeding performance and parental care the hormone prolactin plays a prominent role. Prolactin is a pituitary

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hormone, which rises around the time of egg-laying [28]. High levels are necessary for the initiation and maintenance of diverse breeding behavior [16] such as constant nest attendance [42] and high feeding rate of young [59,62] especially under unfavorable conditions. If a bird is exposed to stress over a longer period, prolactin values start to decrease [19,41]. According to the ‘prolactin stress response hypothesis’ this leads to a reduction of parental care [1] and could ultimately trigger nest desertion [18].

One important parameter leading to a change in prolactin concentration is body condition: heavier common eiders (*Somateria mollissima*) had higher baseline prolactin levels [25], and fasting king penguins (*Aptenodytes patagonicus*) showed a drop in circulating prolactin [20]. The most common pattern described in the literature concerning prolactin and body mass is no obvious relation in good conditioned individuals but increasing body mass loss is linked to decreasing prolactin concentration in starved individuals [24,25,61]. Low body mass and decreasing prolactin is normally accompanied by increasing corticosterone values leading to reduced parental care in order to ensure self maintenance and survival [47].

The association between breeding experience and prolactin or corticosterone level has previously been investigated: In wandering albatrosses (*Diomedea exulans*) and black-browed albatrosses (*Thalassarche melanophris*), Angelier et al. [2 and 4, respectively] demonstrated an age-related change in prolactin and corticosterone but only on population level. In black-browed albatrosses first time breeders had the highest corticosterone concentration [4] whereas it was very low in inexperienced wandering albatrosses [2]. Concerning prolactin, several studies demonstrated an increase of baseline prolactin values during the early breeding career [2–4]. However, Heidinger et al. [40,41] neither showed a relationship between baseline corticosterone and age nor between prolactin concentration and age [41].

To examine the influence of breeding experience on baseline prolactin and corticosterone values, we investigated the common tern *Sterna hirundo*, a small long-lived monogamous seabird with high colony and nest site fidelity [36]. Reproductive performance is known to increase with age in common terns [32,51,52], making them a promising model species to study individual life-histories and age-related changes in diverse traits during reproduction. Due to a unique system to identify birds (fitted with transponders which allow a lifelong automatic identification in the colony) and to take blood samples without catching them [7,12], we can investigate many sexed individuals of known age and breeding experience, breeding history and body condition repeatedly during their breeding career. On this background we are able to study the link of age or experience with hormones on the individual level, which is an improvement of the work on common terns by Heidinger et al. [40,41]. Most other studies on age/experience are cross-sectional, for example by Heidinger et al. [40,41], and there is always a possibility for selection of low reproductive effort phenotypes [33]. This hypothesis could support the progressive disappearance of individuals with high corticosterone levels over time. Therefore it is extremely important to document the change in hormones across years on individual level. Longitudinal studies are very rare, especially in long-lived organisms. With our approach we are able to identify an endocrine maturation with advancing experience rather than a selection of phenotypes.

Based on individuals sampled during incubation between 2006 and 2010, in this paper we address the following questions: (1) Are baseline prolactin and corticosterone levels varying with breeding experience in common terns? (2) Using longitudinal data, can we document a change in hormone concentrations also at the individual level? (3) Is there a sex-dependent difference in hormone levels at any age? (4) Is body mass related to baseline prolactin or corticosterone concentration?

Based on other studies, mainly by Angelier et al. [2–4], we would expect prolactin values to increase during the early breeding career, whereas corticosterone level should decrease as young birds are probably more stressed and less efficient during reproduction. More experienced terns are normally better foragers and should be able to invest more in reproductive performance what could be linked to higher prolactin and lower corticosterone concentration. Since terns show signs of senescence [65], we suggest very old birds to exhibit higher corticosterone and still high prolactin concentration due to an increased effort during breeding.

2. Materials and methods

2.1. Study population and field work

The study was carried out at the common tern colony “Banter See” in Wilhelmshaven, Germany (53°30′40″N, 8°06′20″E) between 2006 and 2010 when colony size was between 350 and 470 breeding pairs. The colony is situated on 6 artificial islands (11 × 5 m), surrounded by low concrete walls equipped with 44 resting boxes. The colony has been studied since 1980, and from 1992 onwards all fledglings were individually marked with a subcutaneously injected microchip (transponder, TROVAN ID 100) in addition to the metal ring. Marked adults and subadults are automatically registered in the colony by special antennas on resting boxes (for details see [10]). Between 1992 and 1995, 101 adults were additionally trapped on the nest and fitted with transponders. During our study period 16–20 of the 44 resting boxes were also equipped with electronic balances (Sartorius TE6100, accuracy ± 1 g), recording weights of birds in addition to identify transponder codes and time of day [81]. Thereby we got body masses of birds for arrival in the colony (mean body mass within the first 4 days in the colony) and during the individual incubation period. Incubation mass was defined as the mean of daily masses between egg laying and hatching of chicks. Terns were sexed by observation of copulations and since 1998 by standard molecular methods [11].

The breeding colony was checked every 2–3 days, new nests were marked and laying dates as well as clutch sizes were recorded [78]. After about 10 days of incubation, each nest was equipped with a mobile antenna for about one day to identify pair mates and assign nest site and breeding parameters to the individuals.

2.2. Blood sampling

Blood samples of breeding common terns were taken in the middle of individual incubation of first clutches (9–14 days after clutch completion). Birds were chosen according to their previous experience in order to cover the whole range of breeding experience in the colony (0–18 years). To minimize the possibility of diurnal variation in prolactin and corticosterone concentration, all blood samples were taken in the early morning between 05:00 and 10:00 a.m. Corticosterone level showed a weak negative correlation with time of day in some years (2007: $r = -0.166$, $P = 0.026$, $N = 180$; 2009: $r = -0.224$, $P = 0.018$, $N = 112$; remaining years: $-0.1 < r < 0.1$, $P > 0.2$), whereas prolactin values were not related to time of day in any sampled season ($r < 0.180$, $P > 0.05$, respectively).

We used starved third stage larvae of blood-sucking bugs in hollow eggs [7,12]. All studied clutches had been equipped with antennas before sampling and after the target bird was identified, we replaced the whole clutch with dummy eggs, one containing the bug [12]. The replaced common tern eggs were kept warm and safe in a box during the sampling procedure. The colony is accustomed to researcher activities, and adults settle down immediately after a person had passed their clutch. After 20–30 min, we

checked if the bug had sucked enough blood (about 300 μ l). If not, we left it for another half hour in the nest but replaced it by a new one in case it was unsuccessful after an hour. Every year the bugs successfully sucked blood in more than 80% of trials.

There was no negative impact of the bug-method on behavior or breeding success of the terns [12]. Immediately after the blood meal, we punctured the bugs abdomen and extracted the blood into a syringe. We kept blood samples cool on ice until centrifugation in the lab (within 4–5 h).

Our validation experiments indicated a strong positive correlation of prolactin values in blood samples obtained by needle and bug in the same individual ($r = 0.696$, $P = 0.017$, $N = 11$). Baseline prolactin was slightly higher in the bug sample (158 ± 10 ng/ml) compared to the one taken by needle (142 ± 7 ng/ml, paired t -test, $t = -2.102$, $P = 0.062$, $N = 11$). This sampling method has also been successfully validated for analyzing corticosterone in common terns [7], blood physiology in birds [9], and hormones [76] or doubly labelled water [75,77] in mammals.

2.3. Hormone assay

Blood samples were centrifuged; the plasma was separated and stored at -20 °C until analysis. Baseline concentrations of prolactin and total (free and bound) corticosterone were measured in the Centre d'Etudes Biologiques de Chizé, France. Plasma level of prolactin was determined twice in each sample by a heterologous radio-immunoassay (RIA) as described in Cherel et al. [20]. Prolactin samples of common terns produced a dose-dependent response curve that paralleled the one of standard chicken plasma (source: Dr. A.F. Parlow, UCLA Medical Center, Los Angeles). Corticosterone value was analyzed in the remaining plasma (normally 25 μ l) via RIA following Lormée et al. [54]. Total plasma corticosterone was measured in samples after ethyl ether extraction using a commercial antiserum, raised in rabbits against corticosterone-3-(Ocarboxy-methyl) oxime bovine serum albumin conjugate (Biogenesis, UK). Cross-reaction was 9% with 1-desoxycorticosterone and less than 0.1% with other plasma steroids. Duplicate aliquots (100 μ l) of the extracts were incubated overnight at 4 °C with 8000 cpm of 3H-Corticosterone (Amersham Pharmacia Biotech-France) and antiserum. The bound and free fractions of corticosterone were separated by adding dextran-coated charcoal. After centrifugation, the bound fraction was counted in a liquid scintillation counter. Minimal detectable corticosterone levels were 0.4 ng/ml (lowest measurement: 0.10 ng/ml). Samples of each year were run in different assays. However, we were able to calculate a correction factor between years because some samples were also analyzed in the assay of the following year. Due to big sample size in some years, corticosterone samples within these years were run in different assays, however, assay identity had no effect on corticosterone levels (2007: Kruskal–Wallis-test: $\chi^2 = 2.462$, $P = 0.482$, $N = 181$, 2008: Mann–Whitney U: $Z = -0.144$, $P = 0.885$, $N = 162$, 2009: Mann–Whitney U: $Z = -0.302$, $P = 0.763$, $N = 120$). Intra- and inter-assay variation for prolactin and corticosterone level was within a range of 6–11% ($n = 4$ duplicates for intra-assay variation).

2.4. Definitions and statistical analyzes

Breeding experience of terns was defined as the number of years the birds had reproduced at 'Banter See' colony before the sampling year (experience at recruitment = 0, range: 0–17 years, see also [50]). The age of first breeding (recruitment age) is 2–5 years in most individuals [57], what leads to a considerable difference in breeding experience within an age group especially in younger breeders. Age of sampled individuals in this study was 2–24 years. Breeding experience and age are nevertheless highly correlated in common terns ($r_s = 0.939$, $P < 0.001$, $N = 345$), but we used only

experience as we know from previous work that it showed a stronger relationship with prolactin and corticosterone levels [4]. Additionally, experience was found to be much more important than age for explaining chick provisioning and reproductive success [52]. Furthermore, within our data set the correlation coefficient of prolactin with breeding experience was slightly higher than with age (experience: $r_s = 0.220$, $P < 0.001$, age: $r_s = 0.186$, $P = 0.001$, $N = 342$) whereas it was comparable in case of corticosterone (experience: $r_s = 0.115$, $P = 0.035$, age: $r_s = 0.122$, $P = 0.033$, $N = 333$). As common terns skip breeding very seldom and show a strong site fidelity [73], most of the difference in experience within an age-group was due to different age at first breeding.

To analyze baseline prolactin and corticosterone level we used a general linear mixed effect model (LME) with the restricted maximum likelihood method (REML). This model can handle repeated measures with unbalanced data subsets due to missing values (individuals were sampled differently often during the study period). The bird's identity was introduced as subject and the sample (1–4, but not every bird has been sampled in four years during the study period) as repeated measure. In case of post hoc comparisons we chose Bonferoni corrections. In a first step all main effects and possible two-way interaction terms were fitted into the model. We then used a stepwise backwards procedure to eliminate non-significant main effects and interactions until only significant terms remained. In case of a significant interaction the main effect was kept in the model even if it had no significant influence.

We analyzed baseline prolactin and corticosterone concentration fitting the particular model with sample, year and sex as factors and breeding experience as well as recruitment age (ranging from 2–5 years) as covariates. In case of prolactin we additionally used experience² because inspection of prolactin data suggested a non-linear relation with breeding experience. This was not true for corticosterone data, however.

For a subsample of 46 birds we could also measure body mass during incubation [50] in one of the sampled years. Additionally, for 237 birds we could measure body mass at arrival in the colony. For these subsets of birds we correlated baseline hormone values with particular body mass by Pearson correlation. This was also used to correlate prolactin and corticosterone levels within an individual. In all correlations every bird occurred only once, chosen by chance. To investigate the early breeding career a paired t -test was used to analyze the difference in baseline prolactin and corticosterone concentration within an individual between the first and second or between the second and third breeding season. Here we used 'residual values' to avoid the year effect masking the effect of breeding experience in this small group of repeated samples (see results). Residual values were calculated for each individual as residual of the mean prolactin and corticosterone value of the seasonal total of sampled birds. Repeatability of hormone values within an individual over years was calculated according to Lessels and Boag [49].

To investigate the relation between breeding experience and both prolactin and corticosterone level for males and females in more detail, we determined the function of mean prolactin and corticosterone depending on experience for both sexes by curve estimation. Best fitting curve (linear, quadratic, cubic) was chosen by highest R^2 and lowest P -value. To test if the relation between experience and hormones was sex-dependent we determined the second derivation of curves for males and females and compared regression coefficient of both lines. Therefore we created a dummy variable (gender: 1 = female, 0 = male) which was entered in a linear regression with experience and their interaction term as predictors for hormone values.

All statistical analyzes were two-tailed, results were expressed as mean \pm 1SD and level of significance was set to $P \leq 0.05$. All analyzes were performed with SPSS 18.

3. Results

3.1. Breeding experience

Breeding experience and experience² had a significantly positive influence on prolactin level (Table 1, Fig. 1a). Additionally, the year had an effect (Table 1) as mean baseline prolactin values in 2006 and 2007 were significantly lower than in 2008–2010 (post hoc comparisons: 2006 vs. 2010: $P = 0.004$, 2006 vs. 2008/2009 and 2007 vs. 2008/2009/2010: $P < 0.001$).

In case of corticosterone, too, we could show a significantly positive effect of breeding experience (Table 2, Fig. 1b) and additionally an influence of experience \times sex and experience \times year (Table 2). The post hoc comparison revealed that males had significantly higher corticosterone values than females ($P = 0.001$), especially in middle aged birds (see Fig. 1b). Furthermore, baseline corticosterone concentration measured during 2007 was significantly lower than during 2006 and 2009 ($P < 0.001$ in both comparisons).

The range of baseline prolactin and corticosterone concentration in inexperienced birds (0–2 years previous experience) was the same as in older birds (prolactin: inexperienced: 26–357 ng/ml, experienced: 25–434 ng/ml; corticosterone: inexperienced: 1–24 ng/ml, experienced: 1–27 ng/ml). In the most experienced terns (≥ 10 years experience) a clear sex-specific development in prolactin values was found: while values in males increased with experience, females showed constantly low levels (Fig 1a). To compare the slopes between males and females we calculated the second derivation of cubic curves for both sexes and compared regression coefficients (linear function: males: $y = 0.756x - 5.312$; females: $y = 0.240x - 2.790$). This analysis revealed that the mean change of prolactin with increasing experience was significantly steeper in males than in females (linear regression, $t = -25.762$, $P = 0.003$, $N = 16$).

3.1.1. Individual-based data early during life

A clear increase of prolactin values in young birds with up to two years breeding experience was found (Fig. 2). We further investigated this increase on individual level: during the early breeding career, terns exhibited increasing residual prolactin

values with every breeding attempt (0 vs. 1 year experience: -34 ± 33 ng/ml vs. -7 ± 58 ng/ml, $t = -1.938$, $P = 0.094$, $N = 9$; 1 vs. 2 years: -25 ± 40 ng/ml vs. 18 ± 41 ng/ml, $t = -2.752$, $P = 0.015$, $N = 17$, Fig. 2) Residual corticosterone values, however, were not significantly different between these early samples (0 vs. 1 year experience: 1.1 ± 2.7 ng/ml vs. 0.3 ± 3.2 ng/ml, $t = 0.594$, $P = 0.571$, $N = 8$; 1 vs. 2 years: 0.3 ± 3.6 ng/ml vs. 0.2 ± 2.3 ng/ml, $t = 0.030$, $P = 0.977$, $N = 17$).

3.2. Body mass

Body mass at arrival in the colony as well as during incubation was significantly and positively correlated with prolactin concentration (arrival mass: $r = 0.135$, $P = 0.037$, $N = 237$; incubation mass: $r = 0.265$, $P = 0.045$, $N = 46$) but not with corticosterone level (arrival mass: $r = -0.093$, $P = 0.165$, $N = 223$; incubation mass: $r = -0.041$, $P = 0.795$, $N = 42$). The positive link between body mass and baseline prolactin level in females was more pronounced than in males (females: arrival mass: $r = 0.196$, $P = 0.033$, $N = 118$; incubation mass: $r = 0.345$, $P = 0.161$, $N = 18$; males: arrival mass: $r = 0.058$, $P = 0.528$, $N = 119$; incubation mass: $r = 0.206$, $P = 0.259$, $N = 32$).

3.3. Hormone interaction and repeatability

Baseline prolactin (188 ± 53 ng/ml, range 25–434 ng/ml) and corticosterone level (6.7 ± 3.7 , range 0.1–27.4 ng/ml) showed a weak but significantly positive correlation within individuals in 2007 ($r_s = 0.155$, $P = 0.037$, $N = 181$). Within the other years the correlations were non-significant ($r_s < 0.2$, $P > 0.1$ in every case). The intra-individual repeatability of prolactin and corticosterone values between samples in different years was very low (original hormone data: prolactin: $F_{213,408} = 1.052$, $r = 0.018$, corticosterone: $F_{201,389} = 1.234$, $r = 0.074$; residual hormone data: prolactin: $F_{213,408} = 1.143$, $r = 0.047$, corticosterone: $F_{201,389} = 1.258$, $r = 0.081$). However, prolactin levels in the second and third measured sample were significantly correlated ($r = 0.295$, $P = 0.001$, $N = 116$). Hormone values between all other samples showed no significant relationship ($r > 0.2$, $P > 0.07$ in all cases).

Table 1
Result of LME analyzing mean baseline prolactin. Statistics are presented for factors, covariates and interaction terms of the last model or at elimination from an earlier model using stepwise backwards approach of non-significant variables ($P > 0.05$). Significant variables are given bold.

Explanatory variable	Final model			Statistics at elimination		
	F	df	P	F	df	P
Experience	25.969	1	<0.001			
Sex				0.001	1	0.986
Sample				0.83t	3	0.378
Year	2.288	4	0.022			
Recruitment age				1.481	1	0.224
Experience ²	14.25	1	<0.001			
Experience \times sex				0.780	1	0.378
Experience \times sample				2.754	3	0.044
Experience \times year	2.352	4	0.052			
Experience \times recruitment age				3.206	1	0.074
Sex \times sample				0.518	3	0.670
Sex \times year				1.418	4	0.226
Sex \times recruitment age				0.259	1	0.611
Sample \times year				0.767	6	0.596
Sample \times recruitment age				0.613	3	0.607
Year \times recruitment age				1.093	4	0.359
Experience ² \times sex				1.357	1	0.244
Experience ² \times sample				1.484	3	0.220
Experience ² \times year	1.352	4	0.251			
Experience ² \times recruitment age				2.048	1	0.153

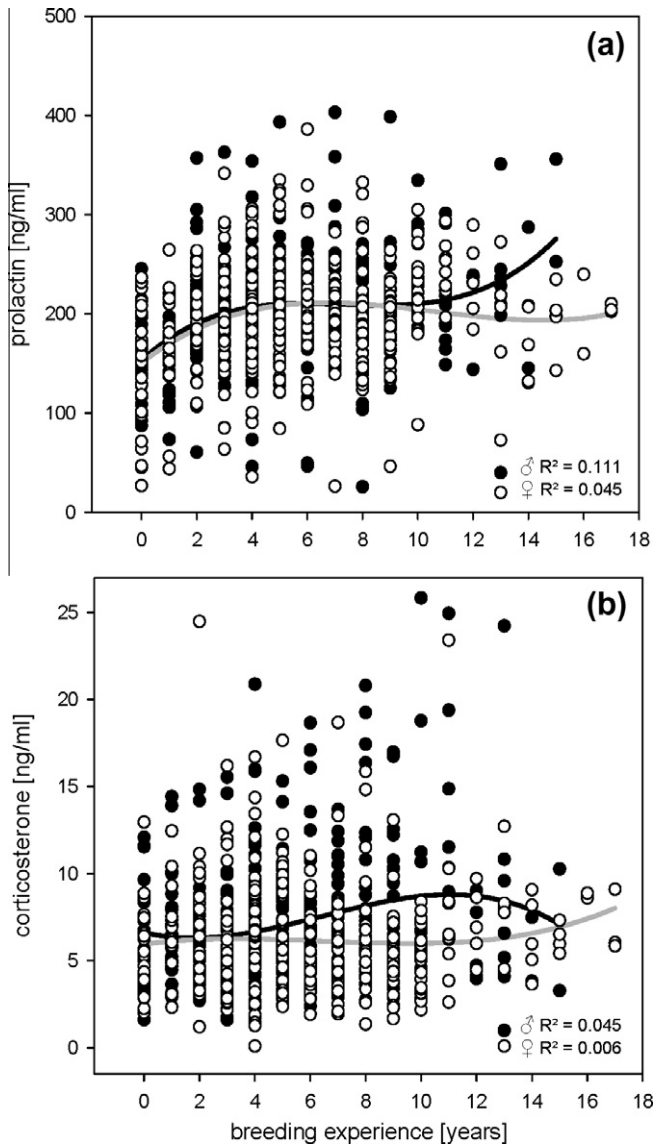


Fig. 1. Mean baseline prolactin (a) and corticosterone (b) level in relation to breeding experience of male (black dots, black line) and female (open dots, grey line) common terns. Cubic R^2 (best fit for the data) is given for both sexes. $N = 375$ males/384 females for prolactin, $N = 361$ males/371 females for corticosterone.

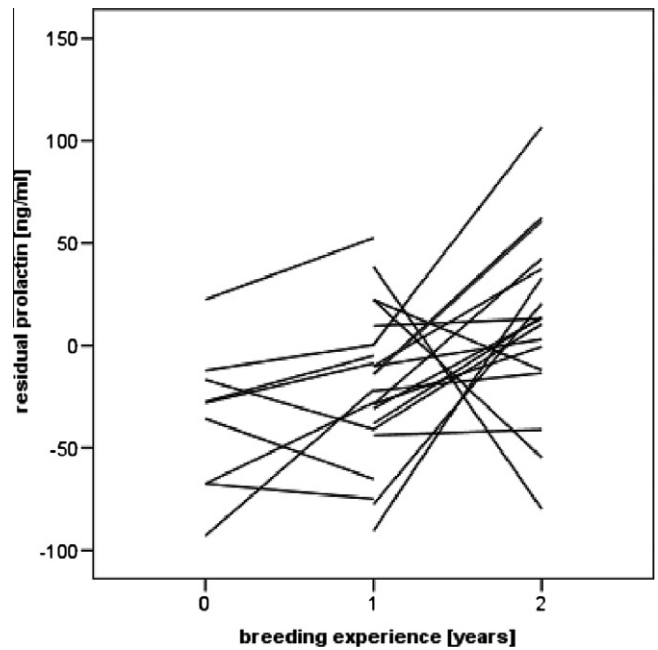


Fig. 2. Individual residual prolactin profiles for terns sampled during their early breeding career. Every line represents one individual; two individuals were even sampled three times. Note that from first to second breeding season three terns showed a decrease in prolactin values, and six an increase. From second to third year only three individuals exhibited a decrease whereas 14 increased residual prolactin.

4. Discussion

4.1. Hormone values and breeding experience

The main focus of this paper was to clarify the link between hormones and breeding experience. We clearly demonstrated that baseline prolactin and corticosterone values were positively affected by breeding experience. In line with our expectation, we showed a clear increase of baseline prolactin level in common terns over the first three breeding attempts at the individual level. Similar results were found in black-browed albatrosses by Angelier et al. [4]. However, compared to other cross-sectional studies investigating prolactin values in relation to breeding experience, we succeeded also in sampling individuals in consecutive seasons during their early breeding career. To the best of our knowledge,

Table 2

Result of LME analyzing mean baseline corticosterone. Statistics are presented for factors, covariates and interaction terms of the last model or at elimination from an earlier model using stepwise backwards approach of non-significant variables ($P > 0.05$). Significant variables are given bold.

Explanatory variable	Final model			Statistics at elimination		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Experience	12.218	1	0.003			
Sex	0.002	1	0.980			
Sample				0.774	3	0.509
Year	0.597	4	0.693			
Recruitment age				0.012	1	0.912
Experience × sex	4.899	1	0.027			
Experience × sample				0.512	3	0.647
Experience × year	4.100	4	0.006			
Experience × recruitment age				0.031	1	0.860
Sex × sample				0.601	3	0.615
Sex × year	1.119	4	0.347			
Sex × recruitment age				0.358	1	0.550
Sample × year				1.065	6	0.383
Sample × recruitment age				0.823	3	0.482
Year × recruitment age				0.610	4	0.656

this is the first study in birds where the increase in baseline prolactin concentration was proven on the individual level.

Elevated prolactin values could either be regarded as a consequence of parental effort or as a stimulator of parental activities [16]. That, in turn, could mean that young birds demonstrate lower parental effort during breeding. This down-regulation of prolactin secretion would prevent inexperienced birds from investing too much in the brood and thereby from hazard their future survival and breeding opportunities [26]. Parents of the California gull (*Larus californicus*) for example increase their parental expenditure with age in terms of feeding, defending and attending the chicks [64]. Low prolactin levels in young terns could be associated with unsteady incubation behavior and longer incubation periods. Stimuli from nest or eggs are necessary to sustain high levels of prolactin [39,79], and if a bird is absent from the nest for too long, this could contribute to a lower prolactin value. That in turn could be one factor leading to the lower reproductive success of inexperienced individuals [52]. Accordingly, Heidinger et al. [41] showed that in young common terns prolactin concentration decreased more rapidly in a stressful situation than it does in older terns. This could lead to frequent interruptions of incubation and subsequently deteriorating reproductive success.

Contrary to our prediction inexperienced common terns had quite low baseline corticosterone levels. According to the “constraint hypothesis” young birds are not able to secrete higher hormone values [26]. However, our results concerning the range of hormone levels showed that some individuals are in fact able to secrete higher corticosterone; only the mean value was low. In contrast to common terns first time breeders of black-browed albatrosses had higher baseline corticosterone levels than experienced birds [4]. Elevated corticosterone values are usually a sign of stress: they are associated with individuals in poor body condition [56] or with low breeding success [45]. But recent studies showed that slightly increased baseline corticosterone levels do not always have negative consequences and lead to brood abandonment [15]. Slightly increased levels could support energy allocation and increase foraging activity [5]. This could even enhance breeding success through an increase of parental provisioning of chicks [30,46,55]. On the other hand, elevated corticosterone levels in more experienced terns might only be the consequence of increased parental stress due to high foraging effort necessary to reproduce successfully.

In experienced common terns we found stable prolactin values with no difference between genders. Baseline corticosterone levels on the other hand increased with advancing experience in males but were consistently low in females. During the first days after hatching in common terns, the father is mainly responsible for feeding the young while the mother stays at the nest [80,82]. Perhaps an elevated baseline corticosterone concentration in males during incubation is a sign of higher activity to find suitable foraging grounds in preparation for the energy consuming chick period (see also Section 4.3). That would be in accordance with the ‘preparative hypothesis’ [66], which claims that corticosterone levels are elevated as preparation for stressful situations.

4.2. Hormone levels amongst the oldest birds

Some studies show that common terns, like many other vertebrates, face reproductive senescence [65], although according to Nisbet et al. [60], old common terns do not show a decrease in reproductive success. In contrast to Heidinger et al. [40,41] our data suggest that hormone values reveal an age-specific change: the group of most experienced terns had higher corticosterone levels compared to younger individuals. Increasing corticosterone with advancing age was also found in old black-browed albatrosses [4] and snow petrels [*Pagodroma nivea*, 38] whereas old wandering

albatrosses had lower baseline corticosterone levels [2]. In both albatross species changing hormone values were accompanied by a decline in breeding success and foraging performance [48]. Elevated baseline corticosterone levels in most experienced terns could be a sign of increased foraging activity [5]. This could be due to a degradation of foraging skills or lower access to resources [17], or to higher parental expenditure because of low residual reproductive value.

Prolactin values, however, exhibited a sex-specific change in most experienced terns: it increased in males but not in females. In the wandering albatross Angelier et al. [2] found a comparable pattern among the oldest birds. Low prolactin levels in female common terns could be either explained by lower maternal expenditure or a decreasing ability to secrete the hormone (physiological senescence). Moreover, a decrease in prolactin concentration could also be linked with a higher density of prolactin receptors [63] and therefore to a higher sensitivity. It could also be related to lower body mass of old females due to declining foraging skills. Heidinger et al. [40] found declining body mass with increasing age in common terns but prolactin level was not analyzed in this study.

We could not clarify why males did not show this decline in prolactin values but perhaps male and female common terns differ in their aging process. Aging can influence the endocrine system and change hormone secretion: for instance in old rats (*rattus spec.*, [71]) and human males [74], the hypothalamo-pituitary-adrenal (HPA) system showed modifications probably due to physiological senescence. Therefore declining prolactin levels in female common terns could indicate senescence. From the age of 15 years onwards decreasing breeding success of terns had been shown [65], when females also start producing smaller eggs [37]. High prolactin values of males, however, could be a mechanism to compensate for reduced female care due to lower prolactin levels in order to keep breeding success, an interesting field for further studies.

4.3. Influence of sex

Baseline prolactin values in common terns were similar between sexes in accordance with an almost equal sharing of parental care between mothers and fathers [35,82]. Shared incubation is common among seabirds, and comparable to our study or the work of Heidinger and co-authors [40,41], Chastel et al. [19] found no sex-specific difference in prolactin concentration of black-legged kittiwakes (*Rissa tridactyla*). In snow petrels, black-browed albatrosses and several tropical species on the other hand, females exhibited higher values than males [2,3,53] despite a comparable amount of parental care. However, the authors could not find an explanation for this circumstance.

Baseline corticosterone concentration showed a sex-dependent pattern: males exhibited higher values than females comparable to snow petrels [38]. In contrast to our results, Heidinger et al. [40,41] found no sex specific difference in corticosterone values in common terns, in line with the results in black-browed albatrosses [4]. Higher corticosterone could indicate a generally increased activity of males [5, see also 4.1], or a higher risk of unpredictable stressors like social challenges (territory defence etc., [14]). Alternatively, the sex-dependent difference in corticosterone concentration could be a sign of sex-specific response to environmental cues or stressors [8].

4.4. Influence of body mass

We found a weak positive link between body mass and baseline prolactin values of common terns whereas corticosterone level was not related to body mass. Heavier common eiders also had higher baseline prolactin [25], or rather prolactin level was negatively correlated to mass loss during incubation [23]. In Goulds Petrels

(*Pagodroma leucoptera*) O'Dwyer et al. [61] could not detect a link between baseline prolactin concentration and body mass during the first incubation bout but showed a positive relation during the second one when petrels are more energy depleted. If birds are in good condition with enough body reserves accumulated they probably do not show a relation with prolactin level, but if body condition deteriorates, prolactin decreases in order to lower parental care and promote self-maintenance [61]. Common terns exhibited a body mass in the normal range of this species (107–160 g, [81]) and did not seem to be energy depleted during our study [27]. In females the link of body mass and prolactin level was more pronounced than in males. Females have to produce the eggs and especially young birds do not recover from this energy-consuming period until mid incubation [9]. This could be accompanied by low body condition and decreased prolactin level.

In accordance with the hypothesis that terns were in good condition is the result that we did not find a negative correlation between body mass and baseline corticosterone levels. In birds with worsening body condition corticosterone rises [45] in order to mobilize energy or increase foraging to promote individual energy balance [47]. Comparable to our study, Criscuolo et al. [25] found no variation in baseline corticosterone value with body mass in incubating common eiders. Chick rearing and failed black-legged kittiwakes also showed no correlation between circulating corticosterone and body mass [19]. On the other hand Heidinger et al. [40] showed a declining corticosterone concentration with decreasing body mass in common terns. In the whole discussion concerning the link between body mass and baseline hormone levels we have to bear in mind that body mass of terns is expressed as mean mass during the total incubation period (about 22 days), implying that it was not necessarily measured at the same day as hormone values.

4.5. Interaction of hormones and repeatability

We demonstrated that birds with a higher baseline prolactin concentration also had an increased baseline corticosterone value, a positive relationship, which was also found in mourning doves (*Zenaidura macroura*) by Miller et al. [58]. However the correlation coefficient was quite low and therefore the relation was not really strong. Other studies showed that prolactin and corticosterone levels act together to control reproductive behavior: experimentally elevated prolactin values caused an increase in corticosterone in ring doves (*Streptopelia risoria*) what could promote feeding of young [46]. In contrast Angelier and Chastel [1] reviewed many studies demonstrating a negative correlation of prolactin and corticosterone concentrations but the authors focused mainly on stress-induced values of corticosterone and not on baseline levels. Koch et al. [46] suggested that elevated prolactin values could counteract the negative effects of high circulating corticosterone during reproduction. If we discuss circulating corticosterone levels we have to take into account that they could also be attenuated or enhanced by corticosterone receptors or corticosterone-binding globulins (CGB, [67]), which we did not analyze in this study.

In birds sampled repeatedly over years, the sample number had no significant effect on either baseline prolactin or corticosterone levels, and repeatability of hormone values was low. Quyang et al. [62] detected also a low repeatability of corticosterone values between years in a passerine bird. In contrast, other studies showed a high repeatability of corticosterone values [6,58]. However, Lynn et al. [58] measured corticosterone twice within a season in eastern bluebirds (*Sialia sialis*) and Angelier et al. [6] compared corticosterone values between two years in black-browed albatrosses. Here however, we measured hormone levels of many birds over 2–4 different years. This possibly leads to higher year-effects on baseline prolactin and corticosterone values which are known to vary considerably between years [2,6,29,69,70]. An-

other possible explanation adding to missing repeatability in hormone values is the connection of hormones with breeding experience, which was the main result of this study. As hormone levels significantly change with increasing experience within an individual, we would not expect high repeatabilities in hormone concentrations between years.

4.6. Conclusions

We showed that prolactin and corticosterone baseline levels were linked to breeding experience in common terns: young individuals had the lowest hormone values but prolactin value increased in inexperienced birds with every breeding attempt, which was also demonstrated on the individual level. Contrarily, baseline corticosterone level increased most pronounced in experienced males. Highly experienced fathers still exhibited increasing prolactin values whereas mothers showed no further increase. A lower prolactin level could be a sign of beginning senescence in female common terns but may be compensated by higher values in male mates. Further work is needed to elucidate the relation of hormones and individual quality in common terns as well as to further investigate the relation with body mass dependent on feeding, e.g. in hungry and satiated terns.

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