What makes a good parent? Sex-specific relationships between nest attendance, hormone levels, and breeding success in a long-lived seabird

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ABSTRACT
Biparental care is found across taxa, but sex-specific contributions vary greatly both between and within species. Factors underlying intraspecific variation may include the phase of the reproductive cycle and sex-specific duties resulting in physiological or environmental constraints that differ between the sexes. For pair members to achieve high breeding success while maintaining good condition, parental duties should be well coordinated between mates. Avian breeding behavior is mediated by hormones such as prolactin and corticosterone, which link the internal and environmental parameters of individuals and regulate resource allocation. Using automated recording at the nest, we analyzed parental attendance by Common Terns (*Sterna hirundo*) in relation to sex, reproductive phase (incubation, chick rearing), time of day, breeding experience, and hormone levels, and related it to reproductive success. Nest attendance of females exceeded that of males, especially at night and during chick rearing. Greater breeding experience was linked to increased attendance at night by males and during incubation by females. Parental nest attendance during incubation was not related to duration of the incubation phase, nor to hatching success. However, fledging success increased with greater parental attendance during the early chick rearing period, reflecting a higher vulnerability of small chicks to mortality compared with eggs. Prolactin values of male parents were significantly lower during chick rearing than incubation and in comparison with values of female parents. Female breeding experience was positively correlated with increased hormone values during chick rearing. Male attendance during chick rearing covaried with hormone levels: moderately increased corticosterone could support males in their new role as feeders by facilitating high activity and foraging effort, whereas lowered prolactin might indicate less contact with chicks and reduced body weight. We show that Common Terns exhibit a flexible system of sex-specific parental care during incubation and chick rearing, reflected in hormone levels, which mediate breeding behavior and ultimately affect reproductive success.

Keywords: nest attendance, parental care, prolactin, corticosterone, Common Tern

¿Qué hace a un buen padre? Relaciones específicas de cada sexo entre el cuidado del nido, los niveles de hormonas y el éxito reproductivo en un ave marina longeva

RESUMEN
El cuidado biparental se encuentra en muchos taxones, pero las contribuciones específicas de cada sexo pueden variar mucho entre y dentro de las especies. Los factores que subyacen la variación interespecífica pueden incluir la fase del ciclo reproductivo y deberes específicos de cada sexo que resultan en limitaciones fisiológicas o ambientales que difieren entre sexos. Para que los miembros de una pareja alcancen un éxito alto mientras mantienen una buena condición, los deberes parentales deben ser bien coordinados entre ellos. El comportamiento reproductivo de las aves está mediado por hormonas como la prolactina y la corticosterona, que enlazan parámetros internos y externos de los individuos y regulan el uso de los recursos. Analizamos el cuidado parental con grabaciones automatizadas de los nidos de *Sterna hirundo* en relación con el sexo, la fase reproductiva (incubación o cría de los polluelos), la hora del día, la experiencia reproductiva y los niveles de hormonas, y lo relacionamos con el éxito reproductivo. El cuidado de los nidos por parte de las hembras excedió el de los machos especialmente en la noche y durante el cuidado de los polluelos. Una mayor experiencia estuvo relacionada con mayor cuidado durante la noche por parte de los machos y durante la incubación por parte de las hembras. El cuidado parental de los nidos durante la incubación no estuvo relacionado con la duración de la fase de incubación ni con el éxito de eclosión. Sin embargo, el éxito de emplumamiento se incrementó con el cuidado de los padres durante el periodo temprano de cría, lo cual refleja una mayor vulnerabilidad de los polluelos pequeños en comparación con los huevos. Los niveles de prolactina de los padres fueron significativamente menores durante la cría que durante la incubación y también en comparación con los valores de las madres. La experiencia de las hembras estuvo correlacionada positivamente con niveles más altos de hormonas durante la cría. El cuidado de los machos durante la cría de los polluelos varió con los niveles hormonales: un incremento moderado en la corticosterona podría facilitar el nuevo rol de los padres como proveedores de

alimento promoviendo mayor actividad y esfuerzo de forrajeo, mientras que la disminución de prolactina podría indicar menos contacto con los polluelos y menor peso corporal. Demostramos que *S. hirundo* tiene un sistema flexible de cuidado parental específico para cada sexo durante la incubación y la cría de los polluelos, lo cual se refleja en niveles hormonales que regulan el comportamiento reproductivo y finalmente afectan el éxito reproductivo.

Palabras clave: corticosterona, cuidado del nido, cuidado parental, prolactina, *Sterna hirundo*

INTRODUCTION

Biparental care can be found across taxa, but is especially widespread in birds, where it is crucial for breeding success (Lack 1968). Incubation and chick feeding duties compete with self-maintenance, requiring cooperation between mates to enable each parent to save energy in order to maximize fitness. This is especially important for long-lived species, for which survival is a primary factor for achieving high lifetime reproductive success (Stearns 1992). Contributions of males and females to biparental care vary greatly between and within species. Moreover, biparental care can be expressed in sex-specific ways, since constraints imposed on males and females by behavioral, physiological, and environmental factors can be very different (Trivers 1972); for example, while courtship feeding can be very demanding for males in terms of food delivery to females (Wendeln and Becker 1999a), egg production bears high costs for females (Heaney and Monaghan 1995, Monaghan et al. 1998, Bauch et al. 2010).

Chick rearing is often assumed to be the most demanding phase of reproduction (Wendeln 1997, Schultner et al. 2013b), and therefore most studies have focused on the rearing period (Whittingham and Dunn 2001). However, producing and incubating eggs, as well as defending the clutch, are also very energy consuming (Monaghan and Nager 1997, Nord and Nilsson 2012). Hence, it is essential to take into account all reproductive phases to gain a more complete understanding of parental investment. Various parameters of parental care have been linked with increased reproductive success in birds. Attentiveness to the clutch during incubation enhances hatching success by reducing the risk of predation (Aldrich and Raveling 1983) and ensures constantly high incubation temperatures (Evans 1989). After hatching, brooding and guarding of chicks is necessary to prevent predation and hypothermia of young (Wang and Buntin 1999). Furthermore, high feeding rates (Quillfeldt 2001, Lewis et al. 2006), as well as high-quality food, are crucial for achieving a good growth rate of chicks and high breeding success (Massias and Becker 1990, Limmer and Becker 2009).

But how is parental care mediated? Hormones play a prominent role, as they link the physiological, behavioral, and environmental parameters of individuals (Wingfield et al. 1998). The pituitary hormone prolactin is essential for the expression of parental care in birds (reviewed by Buntin 1996), and high levels have been shown to stimulate incubation, brooding, and feeding of the young (Buntin et al. 1991). Even in nonbreeding Ringed African Collared-Doves (*Streptopelia roseogrisea risoria*), administration of prolactin together with exposure to squabs initiated breeding behavior (Wang and Buntin 1999). A sharp drop in prolactin level due to decreased body mass or prolonged stress lowered parental care (Boos et al. 2007, Angelier and Chastel 2009) and ultimately induced nest desertion (Spée et al. 2010, 2011). Prolactin is therefore one of the most important hormones to consider in analyses of parental care in birds. But prolactin alone does not trigger a shift in behavior. The main avian glucocorticoid, corticosterone, is known to be involved, too; it has been suggested to mediate allostasis and energy allocation (reviewed by McEwen and Wingfield 2003), and moderately elevated baseline levels increase locomotor activity of birds (Angelier et al. 2007, Corbel and Groscolas 2008), as well as foraging and feeding effort (Bonier et al. 2011, Crossin et al. 2012). Due to these effects, even slight increases in baseline corticosterone levels have been found to result in enhanced reproductive success in birds (Bonier et al. 2009, Ouyang et al. 2011). During prolonged activation of the hypothalamic-pituitary-adrenal (HPA) axis by a stressor, corticosterone may, however, decrease nest attendance (Schultner et al. 2013a) in order to deal with the stressor, ultimately resulting in reduced reproductive success (Groscolas et al. 2008). Therefore, corticosterone has been suggested to mediate the tradeoff between self-maintenance and energy allocation to offspring. In summary, both prolactin and corticosterone vary with internal and environmental factors and interact to regulate breeding behavior (Wingfield et al. 1998, McEwen and Wingfield 2003, Angelier and Chastel 2009).

In this study, we analyzed parental nest attendance during incubation and chick rearing in relation to hatching and fledging success, as well as baseline prolactin and corticosterone levels, in Common Terns (*Sterna hirundo*). The Common Tern is a small, long-lived, and monogamous seabird with biparental care throughout the breeding season (Becker and Ludwigs 2004), yet there is remarkable sex-specific variation in parental care (Nisbet 1973, 2002, Wiggins and Morris 1987, Wendeln 1997). Both parents contribute to incubation and brooding duties, but the female contributes higher proportions of time to incubation, whereas the male is mostly responsible for feeding during early chick rearing while the female stays with the young (Wiggins and Morris 1987, Wendeln 1997). Time of

day may also have an influence on sex-specific incubation behavior: Nisbet (2002) revealed a higher proportion of maternal incubation at night. This small seabird works near capacity throughout the demanding breeding season (Pearson 1968) and is not able to build up body reserves, unlike capital breeders (Boismenu et al. 1992). Therefore, reproductive behavior and success vary with environmental conditions, making the Common Tern a promising model species to study the combined effects of behavior and physiology on reproductive success.

We obtained data from a breeding colony of Common Terns in northern Germany, where numerous life history traits of individuals have been recorded since 1992 (Becker and Wendeln 1997, Zhang et al. 2015) and parental behavior and decisions have been analyzed at both the intra- and inter-individual level. There have been a number of studies conducted in this colony specifically to investigate the influence of hormones on behavior and reproductive success, which form a basis for this work. Riechert et al. (2014a) showed that prolactin levels increased with breeding experience in young Common Terns, which was correlated with improved success during initial breeding attempts. Overall, increased reproductive output was linked with high prolactin levels and slightly increased baseline corticosterone, especially in males (Riechert et al. 2014a). Due to their small body reserves and longevity, sufficient body condition of parents is crucial for breeding behavior: During long fasting bouts on the nest, prolactin decreases while corticosterone increases (Riechert et al. 2014b), a combination that may lead to nest abandonment (Spée et al. 2010, 2011). However, nothing is known about parental roles and breeding behavior during incubation and brooding in relation to hormone levels in this species.

Overall, our paper deals with sex-specific temporal patterns in parental coordination and nest attendance during incubation and chick rearing, and how these patterns are correlated with breeding experience, hormone levels, and reproductive success. Our specific aims were to determine:

(1) Whether parental nest attendance during incubation or chick rearing was related to hatching or rearing success. As chicks are more vulnerable to heat, cold, and rain than eggs (Becker and Ludwigs 2004), we expected a stronger relationship during chick rearing;

(2) Whether nest attendance was influenced by maternal or paternal baseline prolactin and corticosterone levels during incubation or chick rearing. Reduced nest attendance and lower success could partly be driven by low prolactin and high corticosterone values (Spée et al. 2010), and we assumed that we would find a hormonal effect, perhaps more pronounced during the most energy-demanding reproductive phase, the chick rearing period;

(3) How hormones changed between breeding phases at the individual level. Due to different roles after hatching

(Wiggins and Morris 1987), we expected to find lower prolactin and higher corticosterone concentrations in males, but not in females; and

(4) Whether breeding experience affected nest attendance or hormone levels during incubation or chick rearing. From former studies, we know that breeding experience influences foraging success, body mass, and reproductive success (Limmer and Becker, 2007, 2010), and we therefore predicted that inexperienced birds would exhibit lower nest attendance, at least during the demanding chick rearing phase. Breeding experience has been shown to affect hormones as well (Riechert et al. 2012), and we expected a stronger link during chick rearing due to energy constraints, especially in males.

While there are several studies that have related nest attendance to reproductive success or hormone levels in birds (Amundsen 1995, Varpe et al. 2004, Spée et al. 2010, 2011), few studies have integrated physiological and behavioral parameters during incubation and chick rearing at the individual level and related them to reproductive success.

METHODS

Study Site and Species

We conducted our study at the Common Tern colony site "Banter See" in Wilhelmshaven, Germany (53°30′40′′N, 08°06′19′′E), where birds breed on 6 rectangular concrete islands surrounded by a 60-cm high wall. Since 1984, all fledglings have been banded, and, since 1992, additionally fitted with TROVAN ID-100 subcutaneous transponders (Trovan, UK; for details, see Becker and Wendeln 1997). These transponders allow lifelong identification of terns through the use of resting platforms within the colony, where antennas remotely and automatically record and save the individual alphanumeric codes of all birds on the platforms every 5 sec, together with the time of day. Due to the marking program, all birds bred at the colony are of known age. The sex of all birds has also been determined by molecular methods (since 1998) or observation (until 1997). Each breeding season, breeding pairs are identified by putting an antenna around each nest for 1–2 days (usually during midincubation; Becker and Wendeln 1997). The colony is checked 3 times weekly, and new nests are marked, eggs are measured and labeled according to laying order, and newly hatched chicks are banded. At every check, the individual ID and weight of each chick is recorded until fledging (usually within 27 days; Becker and Wink 2003).

Data Collection

Our study was conducted in 4 yr (2008, 2009, 2010, and 2012), in which the number of breeding pairs ranged from 355 to 410 and annual reproductive success averaged 0.33–1.20 chicks per pair. We sampled a total of 41 pairs

TABLE 1. Recorded nest attendance (%), sex-specific nest attendance (SNA), and total nest attendance (TNA) during the day and at night during incubation and chick rearing for male and female Common Terns, and time periods when no bird was recorded and when the system was shut down, in northern Germany.

Nest attendance	Total recordings (%) [a]			
	Incubation day	Incubation night	Rearing day	Rearing night
Males	34 (38)	25 (33)	23 (25)	19 (25)
Females	44 (49)	45 (61)	45 (49)	54 (70)
No one	18 (9)	24 (0)	28 (22)	22 (0)
System shut down	4	6	4	5
SNA				
Males	44	35	34	26
Females	56	65	66	74
TNA				
Pair [b]	86		78	

[a] Numbers in parentheses are corrected values for both sexes assuming that (1) they were incubating the whole night, and (2) they left the clutch during the day when they were not recorded for more than 10 min.
[b] Mean attendance data per pair from values for day and night taking into account the different length of each period.

(2008: $n = 10$, 2009: $n = 15$, 2010: $n = 11$, 2012: $n = 5$) for which both mates were of known age and history. We recorded nest attendance during incubation and chick rearing for 29 pairs, and during chick rearing only for 12 pairs. 'Day' was defined as the duration from sunrise to sunset, and 'night' as the time from sunset to sunrise, using exact data for Wilhelmshaven (www.sunrise-and-sunset.com). Nest attendance of both pair mates was recorded by plate antennas (model AAN FK2, AEG Identifikationssysteme, Ulm, Germany; reading distance up to 24 cm), which were put underneath the nest for several days (average = 9 ± 3 SD days). Around 6 recordings of a bird per min were obtained and used to determine the start and end of each incubation shift. With these values, we built the mean proportion of daytime and nighttime recordings for males and females, time with no parent bird at the nest, and time when the system was shut down for each 24-hr interval. Afterward, periods when the system was shut down were excluded, and a mean value for day and night was calculated for each breeding phase (incubation vs. chick rearing; Table 1).

We analyzed 2 types of nest attendance: (1) Sex-specific nest attendance (SNA), defined as the proportion of time that the male or female was recorded at the nest (Table 1). In this case, time periods when no parent was recorded at the nest were not taken into account. This measure was used to compare nest attendance between the sexes and related to factors such as breeding experience, time of day, and breeding phase; and (2) Total nest attendance (TNA), defined as the proportion of time when at least one member of a pair was registered as present at the nest, also taking into account periods when no parent bird was incubating or brooding (Table 1). In this case, nest attendance was recorded per pair as a measure of parental behavior in relation to breeding success or experience.

Birds may occasionally be quite motionless when incubating, in which case they may not be recorded by the system for several minutes (18–28%; 'no one' in Table 1). To clarify whether birds were still incubating during these periods, we used another set of data collected by scales installed underneath the nest (Riechert et al. 2014b; Appendix). These scales recorded body mass in addition to ID of birds, as well as time of day. Using these data, we found that the presence of breeders was less well recorded (longer gaps between recordings) by the antennas at night than during the day (body mass was recorded by the scales all the time; Appendix Table 6). Furthermore, body weight data showed that terns had significantly shorter periods of absence from the nest during the night than during the day (Wilcoxon test: $Z = -3.82$, $P = 0.02$, $n = 12$), and that a change between mates was reliably recorded by antennas as birds move when they replace each other at the nest during incubation and chick guarding. Moreover, changes between pair mates, as well as the presence or absence of a breeder recorded by the system, showed a high correlation (95%) with behavioral observations (A. Vulcano personal communication). For these reasons, we assumed parents to be incubating the entire night (Table 1), even if gaps in recordings were noticed. In contrast, during the day, terns are known to sometimes leave the clutch unattended for several minutes to defecate, drink, feed, or just rest nearby (Becker and Frank 1990). If these gaps were longer than 10 min, they were treated as time with no parent present (Table 1), which may potentially have led to an underestimation of incubation consistency for Common Terns. For all analyses, we used the corrected calculated attendance data from total recordings for males and females (values in parentheses in Table 1). However, for all these analyses, we note that we did not use behavioral observations, but used antenna recordings to analyze nest attendance.

Antennas were put under the nest 4 ± 2 (mean ± SD) days before the first chick hatched and were left there until 7 ± 2 days after the first chick hatched. All birds accepted this interference at their nests and continued their breeding activities. As Common Tern chicks start to move away from the nest ∼3–4 days after hatching, when parents also start to leave them unattended (Wiggins 1989, Becker and Ludwigs 2004), and are not recorded reliably all day, we restricted our dataset up to the day when the youngest chick was 2 days old. For analyses of SNA, we calculated the mean nest attendance during each phase (incubation and chick rearing) for each sex during the day and night. Likewise, for TNA, the mean value for each phase was calculated per pair.

For each pair, relative hatching and chick rearing success were calculated by subtracting the individual pair's values from the annual colony means of hatching and rearing success, respectively. For rearing success, we used the number of chicks that were alive at day 10 to be able to best relate this metric to nest attendance during the first days of life (until the youngest chick was 2 days old).

Blood Sampling
Blood samples were taken from 39 birds (both members of 17 pairs, plus 5 single pair mates) to analyze hormone levels: (1) From 5 pairs and 4 single pair members, we took a sample only during midincubation (9–15 days after clutch completion); (2) from 2 pairs, we took a sample only during chick rearing (1–5 days after hatching of the first chick); and (3) from 7 pairs and 4 singe pair members, we took samples during both breeding phases. For a subset of 27 of these 39 birds (15 males and 12 females), we were able to measure nest attendance and hormone levels on the same day (for 2 pairs plus 1 single pair member during incubation, 6 pairs plus 4 single pair members during chick rearing, and 3 pairs during both phases).

Blood samples were taken minimally invasively by using blood-sucking bugs (*Dipetalogaster maxima*) in hollow eggs (Becker et al. 2006). Sampling took place in the early morning, between 0500 and 0900 hours, to minimize diurnal variation in hormone levels. Hungry bugs were placed in hollow eggs and, after the target bird was identified as being on the nest by the antenna, the whole clutch was replaced with dummy eggs including the egg containing the bug. Birds resumed incubating immediately. After bugs had finished their meals, ∼20–30 min later, the dummy eggs were retrieved and tern eggs replaced in the nest. Blood was then extracted from the bugs into a syringe. This method has been successfully validated for baseline prolactin (Riechert et al. 2012) and corticosterone (Arnold et al. 2008) and worked well (average success of bugs taking enough blood: 87%; range: 80–97%). Samples were put on ice immediately, and were centrifuged and stored at −20°C within 4–5 hr of collection.

Hormone Analyses
Baseline concentrations of hormones were analyzed at the Centre d'Etudes Biologiques de Chizé, France, by radio-immunoassay (RIA). Following Cherel et al. (1994), prolactin levels were determined twice for each sample after validation for our species and study site (Riechert et al. 2012). Prolactin levels showed a dose-dependent, parallel response curve to the prolactin of chicken plasma (chicken plasma was sourced from the UCLA Medical Center, Los Angeles, California, USA). Total baseline corticosterone level was determined from the remaining plasma (25 μL) after ethyl ether extraction following the methods of Lormée et al. (2003). The lowest corticosterone measurement was 0.42 ng mL^{-1}, while the minimum detection level was 0.10 ng mL^{-1}. Due to a large overall sample size in most years, samples were run in different assays (2008: $n = 4$, 2009: $n = 4$, 2010: $n = 3$, 2012: $n = 2$). However, assay identity had no effect on baseline corticosterone level (Riechert et al. 2012), and the coefficient of variation for intra- and inter-assay variation was within a range of 6–11% ($n = 4$ duplicates of reference sample for intra-assay variation).

Statistics
Analyses of sex-specific nest attendance (SNA). A Wilcoxon test or paired t-test (depending on normality of data) was used to analyze whether the nest attendance of males and females within the pair differed significantly during incubation or chick rearing and during the day vs. at night. A Friedman test further showed whether the sexes varied significantly in their nest attendance depending on reproductive phase and time of day. If a significant difference was detected, we used a Wilcoxon or paired t-test to investigate which periods differed significantly from each other (corrected for multiple comparisons). Pearson or Spearman correlation was chosen to examine the relationship between breeding experience in males and females and mean SNA (total value over the whole breeding period) as well as that of SNA during incubation and chick rearing during daytime and nighttime periods.

We used a linear mixed effects model (LME) with restricted maximum likelihood estimation to analyze SNA in males and females separately, as we sampled both pair members with values summing to 1. Breeding phase (incubation or chick rearing) and time of day (day or night) were included as fixed factors, with breeding experience (number of breeding seasons at the colony before the focal year), prolactin levels, and corticosterone values as covariates. Bird ID and year were included as random effects (most birds occurred in the dataset twice), and the random slope was used to model this effect. LMEs are able to handle repeated and unbalanced data, which was necessary for our dataset as we did not have hormone values or nest attendance data during incubation and chick
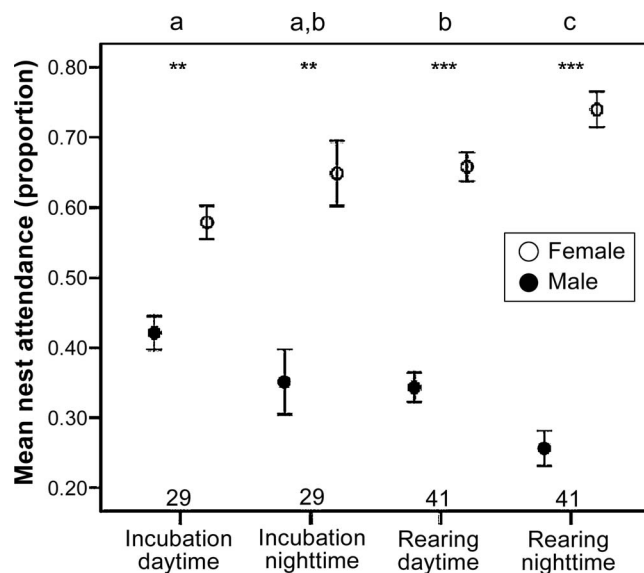
FIGURE 1. Average (± SE) nest attendance (proportion of time) of male (filled circles) and female (open circles) Common Terns during incubation and chick rearing during the day and at night, in northern Germany. Asterisks above error bars indicate significant differences between the sexes (** $P < 0.01$, *** $P < 0.001$), whereas letters mark differences within the sexes. Sample sizes (n) for pairs are presented at the bottom of the graph.

rearing for all birds. No bird was sampled in >1 yr. We fitted the full model with all factors and 2-way interaction terms. Via a stepwise backward elimination procedure, the least significant parameter or interaction term was excluded until only significant variables remained in the model.

Analyses of total nest attendance (TNA) per pair. The same type of model (LME) and selection procedure were used to investigate relative breeding success (hatching and chick rearing) per pair. Breeding phase was included as a fixed factor, with the mean value of total parental nest attendance (TNA) and mean breeding experience per pair as covariates. In addition to year, nest number was used as a random effect to account for the fact that most pairs occurred twice in the dataset (incubation and rearing). TNA during incubation and chick rearing was related to relative hatching and rearing success of pairs, respectively, by Spearman correlation, which was also used to test correlations between incubation duration (days from laying to hatching of the same egg) and TNA during incubation and between TNA during incubation and during rearing. A Wilcoxon test was used to compare the relative success of pairs between the 2 breeding phases.

Analyses of SNA and TNA in relation to hormones. Pearson correlations were used to relate nest attendance during incubation and chick rearing during the day and at night to prolactin and corticosterone levels in both sexes.

We used a subset of 15 males and 12 females for whom blood samples and records of nest attendance were obtained on the same day, as hormone values can show daily variation within the incubation and chick rearing periods (Riechert et al. 2014b). A Pearson correlation was also used to examine the relationship in both hormone values in both breeding phases between pair mates, as well as the change in hormone levels from incubation to chick rearing between them. The change in hormone levels between breeding phases was also correlated with breeding experience in males and females using the same test, which was additionally used to relate prolactin and corticosterone values to relative hatching and rearing success in both sexes. Paired t-tests were used to compare hormone levels in males and females between incubation and chick rearing, as well as between members of the pair in these 2 breeding phases.

Whenever multiple tests were applied to the same dataset, sequential Bonferroni correction (Holm 1979) was used to correct for multiple comparisons. Analyses were performed using SPSS Statistics 23 and 24 (IBM, Armonk, New York, USA), and the level of significance was set to $P \leq 0.05$.

RESULTS

Sex-specific Nest Attendance
Females showed higher nest attendance than males, during both incubation and chick rearing, and during the day and at night (t-test: incubation, daytime: $t = -3.31$, $P = 0.003$, $n = 58$; chick rearing, daytime: $t = -7.58$, $P < 0.001$, $n = 82$; Wilcoxon test: incubation, nighttime: $z = -2.95$, $P = 0.003$, $n = 58$; chick rearing, nighttime: $z = -4.94$, $P < 0.001$, $n = 82$; Figure 1). Breeding experience of females, but not males, showed a tendency to be correlated with mean nest attendance calculated over the whole breeding period ($r = 0.28$, $P = 0.07$, $n = 41$, and $r = 0.16$, $P = 0.32$, $n = 41$, respectively).

Our model selection procedure indicated that variation in nest attendance (SNA) in males was best explained by breeding phase, time of day, and the interaction between time of day and experience (Table 2). Mean male nest attendance was significantly lower during chick rearing at nighttime than during all other phases and times (rearing, daytime: $z = -2.88$, $P = 0.004$, $n = 41$ males; incubation, daytime: $z = -3.99$, $P < 0.001$, $n = 29$; incubation, nighttime: $z = -2.65$, $P = 0.008$, $n = 29$; Figure 1). Moreover, male nest attendance during incubation was significantly higher during the day than at night ($z = -2.26$, $P = 0.02$, $n = 29$) as well as during the day when rearing chicks ($t = -2.59$, $P = 0.02$, $n = 29$). SNA during the day was not related to breeding experience of males ($r = 0.02$, $P = 0.89$, $n = 41$); at night, however, there was a slight tendency for more experienced males to attend the nest for

TABLE 2. Results of a linear mixed effects model analyzing nest attendance by male Common Terns in northern Germany in relation to breeding phase, time of day, breeding experience, and hormones, as well as the interactions between these terms. The best model (after stepwise backward elimination of parameters) is shown on the left-hand side, and parameter values at extraction on the right-hand side. For the variable Year, Wald $Z = 0.84$, $P = 0.38$; and for Bird ID, Wald $Z = 3.07$, $P = 0.04$.

Parameter values of the final model				Parameter values at exclusion from model			
Variable	df	F	P	Variable	df	F	P
Phase	1	9.25	0.01	Experience	1	0.09	0.76
Time	1	5.84	0.03	Corticosterone	1	0.01	0.95
Experience*Time	2	4.24	0.02	Prolactin	1	0.20	0.66
				Phase*Time	1	0.03	0.88
				Phase*Experience	1	3.15	0.09
				Phase*Prolactin	2	0.63	0.56
				Phase*Corticosterone	2	0.47	0.63
				Time*Prolactin	1	0.01	0.92
				Time*Corticosterone	1	0.02	0.91
				Experience*Prolactin	2	0.36	0.43
				Experience*Corticosterone	1	0.64	0.43
				Prolactin*Corticosterone	1	0.59	0.45

a greater proportion of time than less experienced males ($r = 0.37$, $P = 0.15$, $n = 41$), though this difference was far from significant. Hormone values measured during both breeding phases were not found to be significantly correlated with mean SNA in males (Table 2).

For females, the best model contained time of day, breeding phase, and the interaction of breeding experience with breeding phase (Table 3). Female nest attendance differed between breeding phases ($\chi^2_{3,29} = 23.07$, $P < 0.001$), with significantly higher attendance during chick rearing at night than during all other phases and times (incubation, day: $z = -3.73$, $P < 0.001$, $n = 29$ females; incubation, night: $z = -2.39$, $P = 0.02$, $n = 29$; rearing, day: $z = -2.72$, $P = 0.007$, $n = 41$; Figure 1). Moreover, daily nest attendance was significantly lower during daytime incubation than daytime chick rearing ($t = -2.63$, $P = 0.01$, $n = 29$) as well as nighttime incubation ($z = -2.26$, $P = 0.02$, $n = 29$).

During incubation, there was a tendency for more experienced females to exhibit higher nest attendance than less experienced ones ($r = 0.42$, $P = 0.09$, $n = 41$), whereas no relationship was found during chick rearing ($r = 0.12$, $P = 0.27$, $n = 41$). As with males, prolactin and corticosterone values measured in females did not show a significant correlation with SNA during incubation and brooding (Table 3). For both sexes, year of sampling did not contribute significantly to variation in SNA (Tables 2 and 3); however, individual identity explained a significant part of the

TABLE 3. Results of a linear mixed effects model analyzing nest attendance by female Common Terns in northern Germany in relation to breeding phase, time of day, breeding experience, and hormones, as well as their interactions. The best model (after stepwise backward elimination of parameters) is shown on the left-hand side, and parameter values at extraction on the right-hand side. For the variable Year, Wald $Z = 0.68$, $P = 0.50$; and for Bird ID, Wald $Z = 2.47$, $P = 0.04$.

Parameter values of the final model				Parameter values at exclusion from model			
Variable	df	F	P	Variable	df	F	P
Phase	1	6.45	0.03	Experience	1	0.69	0.45
Time	1	3.36	0.04	Corticosterone	1	1.14	0.31
Experience*Phase	2	4.24	0.03	Prolactin	1	0.87	0.70
				Phase*Time	1	0.62	0.45
				Time*Experience	1	2.54	0.13
				Phase*Prolactin	2	0.69	0.42
				Phase*Corticosterone	2	1.47	0.25
				Time*Prolactin	1	1.98	0.23
				Time*Corticosterone	1	0.01	0.95
				Experience*Prolactin	2	1.46	0.24
				Experience*Corticosterone	1	2.81	0.26
				Prolactin*Corticosterone	1	0.27	0.61
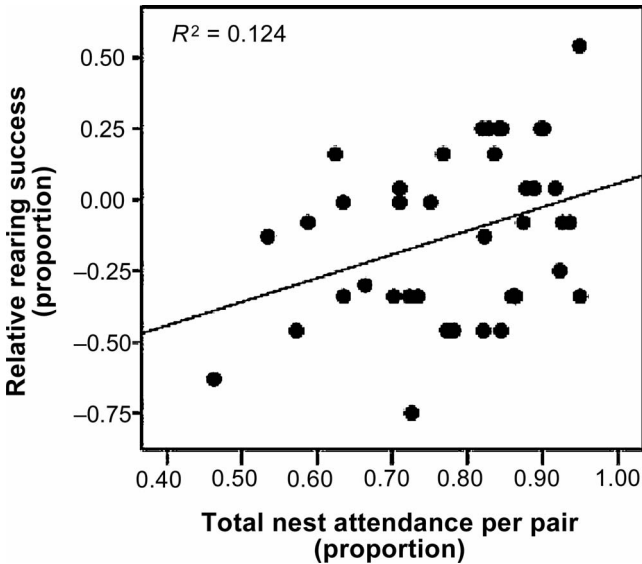
FIGURE 2. Nest attendance per Common Tern pair (proportion of time with one parent present) during chick rearing in relation to the relative number of fledglings (colony mean minus individual data) in northern Germany.

remaining variance in attendance data (Tables 2 and 3), indicating large interindividual variation in nest attendance.

Total Nest Attendance and Breeding Success

Variation in the relative hatching and chick rearing success of pairs was explained by breeding phase, mean experience of pairs, and the interaction between breeding phase and TNA (Table 4). TNA during incubation was quite variable (mean: 0.86 ± 0.10, range: 0.58–0.98), but was not related to hatching success ($r_s = 0.14$, $P = 0.44$, $n = 29$) or incubation duration ($r_s = -0.10$, $P = 0.59$, $n = 29$). During chick rearing, TNA differed between pairs (mean: 0.78 ± 0.12, range: 0.46–0.95), and parents with higher nest attendance during early brood rearing raised significantly more chicks ($r_s = 0.35$, $P = 0.03$, $n = 41$; Figure 2).

Pairs with greater mean breeding experience raised more chicks during early chick rearing than less experienced pairs ($r_s = 0.53$, $P = 0.001$, $n = 41$). For pairs that were sampled during both breeding phases, relative hatching success was significantly higher than relative early chick rearing success (0.13 vs. −0.15, $Z = -3.63$, $P = 0.002$, $n = 29$). Furthermore, parents with high attendance during incubation also showed a tendency to exhibit higher attendance during brood rearing ($r_s = 0.33$, $P = 0.07$, $n = 29$). Nest ID was marginally significant, illustrating differences in success between pairs (Table 4).

Attendance Patterns and Hormone Levels

Using a subset of data with synchronous measurements of hormones and nest attendance within 1 day (to account for seasonal variation in hormone levels), we found no significant correlation between prolactin or corticosterone level and nest attendance during incubation or chick rearing for either sex (incubation: males, $r < 0.5$, $P > 0.3$, $n = 5$; females, $-0.3 < r < 0.0$, $P > 0.6$, $n = 6$; rearing: males, $-0.3 < r < 0.0$, $P > 0.4$, $n = 13$; females, $-0.1 < r < 0.0$, $P > 0.9$, $n = 9$). However, taking into account time of day and breeding phase, a pattern was revealed: In the chick rearing phase, during the day, males with elevated prolactin levels exhibited slightly higher nest attendance ($r = 0.51$, $P = 0.07$, $n = 13$; Figure 3A). In addition, males with elevated baseline levels of corticosterone tended to show lower daytime nest attendance ($r = -0.51$, $P = 0.08$, $n = 13$; Figure 3B). However, for males during incubation and for females during both breeding phases, we did not find a significant correlation of either hormone with nest attendance ($-0.5 < r < 0.5$, $P > 0.1$, $4 < n < 10$).

Corticosterone values did not change between the breeding phases in either sex, and nor did prolactin values in females (Table 5). Males, on the other hand, exhibited significantly lower prolactin values during chick rearing compared with incubation (Table 5).

Prolactin values during both phases, as well as corticosterone values during incubation, were not significantly correlated between pair members ($r < 0.5$, $P > 0.3$, $n = 7$). During rearing of chicks, however, a trend toward a negative correlation between corticosterone values of pair members was found ($r = -0.72$, $P = 0.07$, $n = 7$). Regarding the change in hormones between the 2 breeding phases, values for pair members were not significantly related to each other ($r < 0.3$, $P > 0.5$, $n = 7$).

TABLE 4. Results of a linear mixed effect model analyzing pair breeding success of Common Terns in northern Germany in relation to breeding phase, total nest attendance (TNA), and breeding experience, as well as the interactions between these terms. The best model (after stepwise backward elimination of parameters) is shown on the left-hand side, and parameter values at extraction on the right-hand side. For the variable Year, Wald $Z = 1.90$, $P = 0.13$; and for Nest ID, Wald $Z = 2.51$, $P = 0.07$.

Parameter values of the final model				Parameter values at exclusion from model			
Variable	df	F	P	Variable	df	F	P
Phase	1	7.06	0.01	TNA	1	1.97	0.17
Experience	1	7.55	0.008	Phase*Experience	2	0.54	0.47
Phase*TNA	2	4.04	0.04	TNA*Experience	1	0.03	0.87
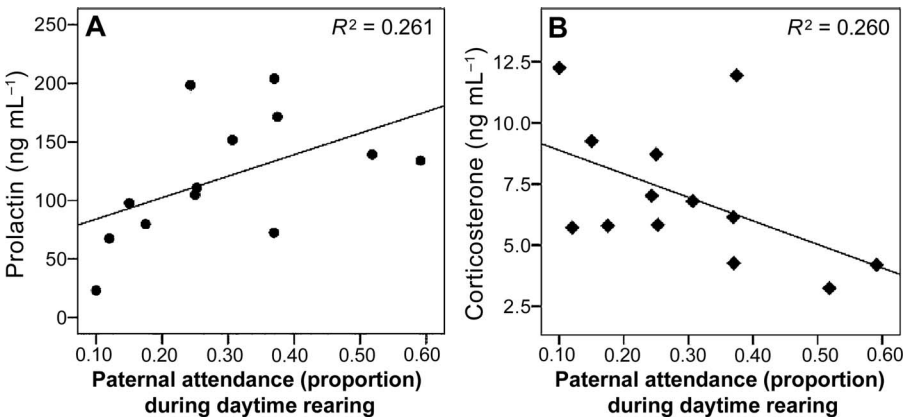
FIGURE 3. (**A**) Baseline prolactin (ng mL^{-1}) and (**B**) baseline corticosterone (ng mL^{-1}) of male Common Terns in relation to nest attendance during daytime chick rearing, in northern Germany.

In females, but not males, greater breeding experience was positively correlated with a change in prolactin values from incubation to chick rearing (females: $r = 0.78$, $P = 0.04$, $n = 7$; males: $r = -0.26$, $P = 0.50$, $n = 11$). Similarly, in the case of corticosterone, greater experience in females, but not males, was marginally significant and slightly positively correlated with an increase from incubation to chick rearing (females: $r = 0.68$, $P = 0.09$, $n = 7$; males: $r = -0.21$, $P = 0.55$, $n = 11$). We did not find any correlation between prolactin or corticosterone and hatching or rearing success in males or females ($-0.4 < r_s < 0.3$, $P > 0.3$ in every case, $n = 11$ and 7 for males and females, respectively).

DISCUSSION

In birds with biparental care, good coordination of parental duties in order to enhance attendance of eggs and chicks is essential to maximize reproductive success (Lack 1968). Incubation and brooding duties compete with foraging, and, in long-lived species for which survival is important for lifetime reproductive success, synchronization of parental duties is crucial for parents to maintain sufficient body condition as well as high breeding success (Stearns 1992). In Common Terns, we

showed that high parental nest attendance early in the chick rearing phase increased fledging success and that, in males, nest attendance was related to increased prolactin and decreased corticosterone levels. The underlying mechanism is suggested to be hormones linking environmental factors with individual body condition and adjusting breeding behavior accordingly (Wingfield et al. 1998). Here, we discuss the causes and consequences of the observed sex-specific differences in nest attendance of Common Terns, addressing aspects of behavior, breeding experience, and the hormones prolactin and corticosterone. However, we note that our sample sizes for single years were quite low and therefore our statistical power was limited.

Sex- and Phase-dependent Daytime and Nighttime Nest Attendance
Consistent with the findings of previous studies (Wiggins and Morris 1987, van der Winden 2005), our results clearly confirm sex-specific parental care in Common Terns: Females spent a greater proportion of time incubating eggs and brooding small chicks than their mates. This pattern was especially pronounced at night (see also Nisbet 2002), as has also been found in Western Gulls (*Larus occidentalis*; Pierotti 1981). This pattern is not universal,

TABLE 5. Hormone concentrations (ng mL^{-1}; PRL = prolactin, CORT = corticosterone) per breeding phase and pair mate of Common Terns in northern Germany. A *t*-test for related samples was used; significant *P*-values are highlighted in bold font.

Hormone	Mate	n	Incubation	Rearing	t (P)
			Phase		
PRL	Male	11	200.0	120.7	4.52 (**0.001**)
	Female	7	212.7	208.4	0.12 (0.90)
	t (P) between paired mates	7	−0.27 (0.89)	−3.33 (**0.01**)	
CORT	Male	11	6.5	6.8	−0.23 (0.78)
	Female	7	6.0	6.8	−0.58 (0.58)
	t (P) between paired mates	7	0.39 (0.68)	0.06 (0.97)	

however, and can be reversed, as is found in Black Terns (*Chlidonias niger*; van der Winden 2005), Thick-billed Murres (*Uria lomvia*; Jones et al. 2002), and various sandpipers (Byrkjedal 1985, Bergstrom 1986, Warnock and Oring 1996). However, we assume that male Common Terns often rest near the nest while the female is incubating (see also Wiggins and Morris 1987, Weidinger 1998, Nisbet 2002). But is the pattern of female-biased Common Tern nest attendance a general one, or might sex-specific parental attendance change under certain conditions? Common Terns are not able to defend their eggs or chicks against nocturnal predators (Wendeln and Becker 1999b, Nisbet 2002), and it would be particularly interesting to analyze parental attendance under the pressure of nocturnal predation.

Comparable with the results of prior studies of Common Terns (Wiggins and Morris 1987, Burness et al. 1994, Galbraith et al. 1999) and Black Terns (van der Winden 2005), and in line with our prediction, males were rarely detected on the nest after young hatched. During the first week of chick rearing, the female mostly stayed with the chicks, while the male predominantly foraged and fed the young (Wiggins and Morris 1987, Wendeln 1997). Accordingly, the feeding rate, which is normally ∼1 food item per chick per hour in this colony (Frank 1992), was found to be much higher in males than in females (Wendeln 1997). The lower nest attendance of males during incubation may allow them more time to find and exploit suitable foraging grounds (Becker et al. 1993, Wendeln 1997), in order to be prepared and save time and energy once the chicks hatch and have to be fed regularly and frequently with larval fish.

In line with our expectation, the breeding experience of Common Terns did affect nest attendance. Older females spent more time at the nest during incubation than younger ones, and more experienced males exhibited increased nest attendance at night. It is known that Common Terns need several years to become proficient at foraging and chick provisioning (Limmer and Becker 2009, 2010), and therefore more experienced birds are able to spend more time at the nest. However, as mentioned previously, we assume that males stay close to the nest even when they are not incubating or brooding. Females might have a stronger drive to incubate than males, possibly leading to the fact that experienced females increase nest attendance during incubation, while males rest near the nest after foraging.

Year did not have a significant effect on nest attendance, illustrating that, on average, Common Terns maintain constant breeding behavior under different conditions. Other factors, such as experience and quality of the pair, have a much greater effect on breeding behavior.

Reproductive Success and Nest Attendance

Low parental attentiveness to the clutch can prolong the incubation period and increase the risk of predation (Aldrich and Raveling 1983, Pienkowski 1984). Parental attendance at the nest was quite variable between Common Tern pairs; however, interpair variability was not related to hatching success or incubation duration. Though linked to parental quality (Wendeln and Becker 1999a), hatching success in the Banter See colony was relatively high overall during the years of this study (Riechert et al. 2014a). This could be one reason for no link being found with nest attendance. Another reason could be the fact that eggs hatch even after being left unattended for periods of time (Sudmann et al. 1994, Stoleson and Beissinger 1999), supported by the finding that embryos of Common Terns and many waders are quite robust to fluctuations in temperature (Myhre and Steen 1979). Egg predation of unattended clutches during the day is rare in the Banter See colony (Becker 1998). Only complete nights without incubation due to nocturnal predator activity led to prolonged incubation and decreased hatching success (Sudmann et al. 1994, Wendeln and Becker 1999b).

In line with our prediction, parental nest attendance during chick rearing was positively correlated with rearing success up to day 10, which was much more variable than hatching success. Our recording of nest attendance was restricted to only the first days of the rearing period, until the smallest chick was 2 days old. This is the period when the semiprecocial chicks need to be brooded by the parents (Nisbet 2002, Becker and Ludwigs 2004). There are many more factors that affect fledging success, such as feeding rate and food quality (Massias and Becker 1990, Quillfeldt 2001). However, high nest attendance during the first few days may reflect high individual quality, contributing to early chick survival in various ways and thereby enhancing breeding success. Similarly, chick survival in the Antarctic Petrel (*Thalassoica antarctica*) was high after constant guarding by parents, even beyond thermoregulatory needs (Varpe et al. 2004). Furthermore, chicks of the Snow Petrel (*Pagodroma nivea*) that were left alone at day 4 exhibited lower growth rates and survival than chicks that were abandoned at an older age, reflecting low parental quality (Amundsen 1995). Besides exposure to hunger, rain, or cold, Common Tern chicks at Banter See that are left alone can be attacked by neighbors in this dense breeding colony, and sometimes die due to their injuries (J. Riechert and P. Becker personal observations).

Breeding success did not differ significantly between years in this study. Other studies of seabirds have found clear effects of year on reproductive success (e.g., Becker 1998, Quilllfeldt 2001, Golet et al. 2004) and, in a previous study, we also showed that reproductive success was significantly different between years in this Common Tern

colony (Riechert et al. 2014a). However, sample sizes were much higher in these studies.

Influence of Hormone Levels on Nest Attendance

Because hormone levels exhibit diurnal variation (Lea et al. 1982, Romero and Remage-Healey 2000) and were only measured during the day, we restricted our analyses to daytime nest attendance patterns. Prolactin levels have been suggested to be directly linked to the amount of parental care (reviewed by Angelier and Chastel 2009), and sex-specific parental care has been shown to be reflected in prolactin values: The sex that contributed more to incubation or rearing of young exhibited higher prolactin levels during the respective breeding phase (Lormée et al. 2000, Schmid et al. 2011). In line with our prediction, we found that prolactin values after hatching were reduced in males, but not in females, and that males with reduced prolactin values exhibited lower nest attendance. Likewise, male and female Black-legged Kittiwakes (*Rissa tridactyla*), which spend much time at sea resulting in reduced nest attendance, exhibit low prolactin values (Angelier et al. 2009).

High parental effort could lead to reduced body reserves, reflected in low prolactin values, as shown in kittiwakes and Adelie Penguins (*Pygoscelis adeliae*), ultimately lowering nest attendance (Angelier et al. 2009, Spée et al. 2010). Consistent with this finding, from a prior study we know that Common Terns with a considerable loss in body mass due to a long incubation bout are characterized by decreased prolactin values compared with their satiated state (Riechert et al. 2014b). The current study has linked this result with nest attendance, demonstrating that lower prolactin values are accompanied by reduced nest attendance. Due to high foraging effort, males might lose more weight than females, and their contact with chicks is lower, which is reflected in lower prolactin values after hatching.

Parents with low nest attendance during chick rearing were characterized not only by low prolactin, but also by increased baseline corticosterone, matching our prediction. This is the next step and logical consequence of the preceding study (Riechert et al. 2014b), which demonstrated low prolactin and increased corticosterone in birds with low body condition. Experimentally increased corticosterone levels resulted in lower nest attendance of kittiwakes as well (Kitaysky et al. 2001, Angelier et al. 2009). Moderately elevated corticosterone is known to trigger activity (Astheimer et al. 1992, Angelier et al. 2007), and increase foraging effort (Kitaysky et al. 2001, Crossin et al. 2012) and feeding of young (Koch et al. 2002, Doody et al. 2008, Bonier et al. 2009). Common Terns caring for chicks show high parental effort (Wendeln and Becker 1999b), which has been linked with elevated baseline corticosterone values in several species (Harding et al. 2009, Miller et al. 2009, Bonier et al. 2011). On the other hand, elevated corticosterone achieved by implantation and reaching the stress level is known to negatively affect reproduction (reviewed by Angelier and Chastel 2009). Common Terns were characterized by lower body mass and increased corticosterone levels at the end of an incubation bout compared with the start of the incubation bout (Riechert et al. 2014b). In line with this, in Dovekies (*Alle alle*), experimental evidence has been found that increasing mass loss results in elevated baseline corticosterone values in both sexes (Harding et al. 2009). As Common Terns lose much more body mass during chick rearing than incubation (Wendeln and Becker 1996, Wendeln 1997), their increased corticosterone levels could indicate low reserves and may stimulate foraging and food intake.

Hormone values were not significantly correlated between pair members, except those of corticosterone during chick rearing, which showed a negative correlation. This could indicate that higher foraging activity in males, reflected in enhanced corticosterone values, might lead to lower activity in females, as males might provision the young sufficiently.

While rearing chicks, experienced females exhibited increased prolactin and corticosterone values compared with younger females. From previous studies in this colony, we know that greater experience can be linked with increased foraging success and body weight (Limmer and Becker 2007, 2009). Riechert et al. (2014b) indicated that the change in hormones is more pronounced under stronger energy constraints during chick rearing compared with incubation, which is also illustrated by the present study that additionally integrated data on breeding behavior to complete the picture.

During chick rearing, we found a much stronger relationship between hormone levels and nest attendance in males compared with females. This is in line with the results of Wiggins and Morris (1987), Burness et al. (1994), and Wendeln (1997), who all showed higher feeding effort by male Common Terns, especially during the first week of rearing. On the other hand, females were more constrained in their own feeding than males, as they were engaged in breeding activities most of the time, reflected in their high mass loss during rearing of chicks (Wendeln and Becker 1996, Wendeln 1997). Parental maintenance is further hampered by the marine environment of the Wadden Sea, where foraging success depends on the tidal cycle (Frank and Becker 1992). Higher male activity and foraging effort in line with the new role as feeder after hatching of chicks is reflected in reduced nest attendance, lower baseline prolactin levels, and increased corticosterone values. In this respect, the current study integrates measures of

behavior and hormonal data into the already existing data on body condition, breeding experience, reproductive success, and hormone values, thereby completing the picture of the regulation of breeding in Common Terns.

Conclusions

We integrated measures of nest attendance, reproductive success, and hormonal status during incubation and chick rearing in Common Terns, enabling a more detailed insight into the regulation of avian breeding behavior. Different parental roles were indicated by sex-specific temporal patterns based on interactions between hormones and nest attendance during incubation and rearing, modified by the breeding experience of the parents. Further studies should address whether sex-specific nest attendance and vulnerability may change under adverse environmental conditions, such as the presence of nocturnal predators. Investigations during the later stages of chick rearing should clarify if females, like males, exhibit changes in hormone levels when they start extensively feeding chicks as well. Furthermore, it would be interesting to analyze intraindividual plasticity in behavior by comparing parental care, hormones, and reproductive success from favorable and unfavorable breeding seasons.

LITERATURE CITED

Aldrich, T. W., and D. G. Raveling (1983). Effects of experience and body weight on incubation behavior of Canada Geese. The Auk 100:670–679.

Amundsen, T. (1995). Egg size and early nestling growth in the Snow Petrel. The Condor 97:345–351.

Angelier, F., and O. Chastel (2009). Stress, prolactin and parental investment in birds: A review. General and Comparative Endocrinology 163:142–148.

Angelier, F., C. Clément-Chastel, J. Welcker, G. W. Gabrielsen, and O. Chastel (2009a). How does corticosterone affect parental behaviour and reproductive success? A study of prolactin in Black-legged Kittiwakes. Functional Ecology 23:784–793.

Angelier, F., S. A. Shaffer, H. Weimerskirch, C. Trouvé, and O. Chastel (2007). Corticosterone and foraging behavior in a pelagic seabird. Physiological and Biochemical Zoology 80:283–293.

Arnold, J. M., S. A. Oswald, C. C. Voigt, R. Palme, A. Braasch, C. Bauch, and P. H. Becker (2008). Taking the stress out of blood collection: Comparison of field blood-sampling techniques for analysis of baseline corticosterone. Journal of Avian Biology 39:588–592.

Astheimer, L. B., W. A. Buttemer, and J. C. Wingfield (1992). Interactions of corticosterone with feeding, activity and metabolism in passerine birds. Ornis Scandinavica 23:355–365.

Bauch, C., S. Kreutzer, and P. H. Becker (2010). Breeding experience affects condition: Blood metabolite levels over the course of incubation in a seabird. Journal of Comparative Physiology B 180:835–845.

Becker, P. H. (1998). Langzeittrends des Bruterfolgs der Flussseeschwalbe Sterna hirundo und seiner Einflussgröen im Wattenmeer. Vogelwelt 119:223–234.

Becker, P. H., and D. Frank (1990). Kontinuierliche Wägung brütender Seevögel zur Analyze der Ernährungssituation. Proceedings of the 100th International DO-G Meeting Bonn 1988:173–179.

Becker, P. H., and J.-D. Ludwigs (2004). Sterna hirundo, Common Tern. BWP Update 6:91–137.

Becker, P. H., and H. Wendeln (1997). A new application for transponders in population ecology of the Common Tern. The Condor 99:534–538.

Becker, P. H., and M. Wink (2003). Influences of sex, sex composition of brood and hatching order on mass growth in Common Terns Sterna hirundo. Behavioral Ecology and Sociobiology 54:136–146.

Becker, P. H., D. Frank, and S. R. Sudmann (1993). Temporal and spatial patterns of Common Tern (Sterna hirundo) foraging in the Wadden Sea. Oecologia 93:389–393.

Becker, P. H., C. C. Voigt, J. M. Arnold, and R. Nagel (2006). A non-invasive technique to bleed incubating birds without trapping: A blood-sucking bug in a hollow egg. Journal of Ornithology 147:115–118.

Bergstrom, P. W. (1986). Daylight incubation sex roles in Wilson's Plover. The Condor 88:113–115.

Boismenu, C., G. Gauthier, and J. Larochelle (1992). Physiology of prolonged fasting in Greater Snow Geese (Chen caerulescens atlantica). The Auk 109:511–521.

Bonier, F., I. T. Moore, P. R. Martin, and R. J. Robertson (2009). The relationship between fitness and baseline glucocorticoids in

a passerine bird. General and Comparative Endocrinology 163:208–213.

Bonier, F., I. T. Moore, and R. J. Robertson (2011). The stress of parenthood? Increased glucocorticoids in birds with experimentally enlarged broods. Biology Letters 7:944–946.

Boos, M., C. Zimmer, A. Carriere, J.-P. Robin, and O. Petit (2007). Post-hatching parental care behaviour and hormonal status in a precocial bird. Behavioural Processes 76:206–214.

Buntin, J. D. (1996). Neural and hormonal control of parental behavior in birds. In Parental Care: Evolution, Mechanisms, and Adaptive Significance (J. S. Rosenblatt and C. T. Snowdon, Editors). Advances in the Study of Behavior 25: 161–213.

Buntin, J. D., G. M. Becker, and E. Ruzycki (1991). Facilitation of parental behavior in Ring Doves by systemic or intracranial injections of prolactin. Hormones and Behavior 25:424–444.

Burness, G. P., R. D. Morris, and J. P. Bruce (1994). Seasonal and annual variation in brood attendance, prey type delivered to chicks, and foraging patterns of male Common Terns (*Sterna hirundo*). Canadian Journal of Zoology 72:1243–1251.

Byrkjedal, I. (1985). Time-activity budget for breeding Greater Golden-Plovers in Norwegian mountains. The Wilson Bulletin 97:496–501.

Cherel, Y., R. Mauget, A. Lacroix, and J. Gilles (1994). Seasonal and fasting-related changes in circulating gonadal steroids and prolactin in King Penguins, *Aptenodytes patagonicus*. Physiological Zoology 67:1154–1173.

Corbel, H., and R. Groscolas (2008). A role for corticosterone and food restriction in the fledging of nestling White Storks. Hormones and Behavior 53:557–566.

Crossin, G. T., P. N. Trathan, R. A. Phillips, K. B. Gorman, A. Dawson, K. Q. Sakamoto, and T. D. Williams (2012). Corticosterone predicts foraging behavior and parental care in Macaroni Penguins. The American Naturalist 180:E31–E41.

Doody, L. M., S. I. Wilhelm, D. W. McKay, C. J. Walsh, and A. E. Story (2008). The effects of variable foraging conditions on Common Murre (*Uria aalge*) corticosterone concentrations and parental provisioning. Hormones and Behavior 53:140–148.

Evans, R. M. (1989). Effect of low incubation temperature during the pipped-egg stage on hatchability and hatching times in domestic chickens and Ring-billed Gulls. Canadian Journal of Zoology 68:836–840.

Frank, D. (1992). The influence of feeding conditions on food provisioning of chicks in Common Terns *Sterna hirundo* nesting in the German Wadden Sea. Ardea 80:45–55.

Frank, D., and P. H. Becker (1992). Body-mass and nest reliefs in Common Terns *Sterna hirundo* exposed to different feeding conditions. Ardea 80:57–69.

Galbraith, H., J. J. Hatch, I. C. T. Nisbet, and T. H. Kunz (1999). Age-related changes in efficiency among breeding Common Terns *Sterna hirundo*: Measurements of energy expenditure using doubly-labelled water. Journal of Avian Biology 30:85–96.

Golet, G. H., J. A. Schmutz, D. B. Irons, and J. A. Estes (2004). Determinants of reproductive costs in the long-lived Black-legged Kittiwake: A multiyear experiment. Ecological Monographs 74:353–372.

Groscolas, R. A., A. Lacroix, and J.-P. Robin (2008). Spontaneous egg or chick abandonment in energy-depleted King Penguins: A role for corticosterone and prolactin? Hormones and Behavior 53:51–60.

Harding, A. M. A., A. S. Kitaysky, W. E. Hall, J. Welcker, N. J. Karnovsky, S. L. Talbot, K. C. Hamer, and D. Grémillet (2009). Flexibility in the parental effort of an Arctic-breeding seabird. Functional Ecology 23:348–358.

Heaney, V., and P. Monaghan (1995). A within-clutch trade-off between egg production and rearing in birds. Proceedings of the Royal Society of London, Series B 261:361–365.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65–70.

Jones, I. L., S. Rowe, S. M. Carr, G. Fraser, and P. Taylor (2002). Different patterns of parental effort during chick-rearing by female and male Thick-billed Murres (*Uria lomvia*) at a low-Arctic colony. The Auk 119:1064–1074.

Kitaysky, A. F., J. C. Wingfield, and J. F. Piatt (2001). Corticosterone facilitates begging and affects resource allocation in the Black-legged Kittiwake. Behavioral Ecology 12:619–625.

Koch, K. A., J. C. Wingfield, and J. D. Buntin (2002). Glucocorticoids and parental hyperphagia in Ring Doves (*Streptopelia risoria*). Hormones and Behavior 41:9–21.

Lack, D. (1968). Ecological Adaptations for Breeding in Birds. Methuen, London, UK.

Lea, R. W., P. J. Sharp, and A. Chadwick (1982). Daily variations in the concentrations of plasma prolactin in broody bantams. General and Comparative Endocrinology 48:275–284.

Lewis, S., S. Wanless, D. A. Elston, M. Duhr Schultz, E. Mackley, M. Du Toit, J. G. Underhill, and M. P. Harris (2006). Determinants of quality in a long-lived colonial species. Journal of Animal Ecology 75:1304–1312.

Limmer, B., and P. H. Becker (2007). The relative role of age and experience in determining variation in body mass during the early breeding career of the Common Tern (*Sterna hirundo*). Behavioral Ecology and Sociobiology 61:1885–1896.

Limmer, B., and P. H. Becker (2009). Improvement in chick provisioning with parental experience in a seabird. Animal Behaviour 77:1095–1101.

Limmer, B., and P. H. Becker (2010). Improvement of reproductive performance with age and breeding experience depends on recruitment age in a long-lived seabird. Oikos 117:60–68.

Lormée, H., P. Jouventin, A. Lacroix, J. Lallemand, and O. Chastel (2000). Reproductive endocrinology of tropical seabirds: Sex-specific patterns in LH, steroids, and prolactin secretion in relation to parental care. General and Comparative Endocrinology 117:413–426.

Lormée, H., P. Jouventin, C. Trouvé, and O. Chastel (2003). Sex-specific patterns in baseline corticosterone and body condition changes in breeding Red-footed Boobies *Sula sula*. Ibis 145:212–219.

Massias, A., and P. H. Becker (1990). Nutritive value of food and growth in Common Tern *Sterna hirundo* chicks. Ornis Scandinavica 21:187–194.

McEwen, B. S., and J. C. Wingfield (2003). The concept of allostasis in biology and biomedicine. Hormones and Behavior 43:2–15.

Miller, D. A., C. M. Vleck, and D. L. Otis (2009). Individual variation in baseline and stress-induced corticosterone and prolactin levels predicts parental effort by nesting Mourning Doves. Hormones and Behavior 56:457–464.

Monaghan, P., and R. G. Nager (1997). Why don't birds lay more eggs? Trends in Ecology & Evolution 12:270–274.

Monaghan, P., R. G. Nager, and D. C. Houston (1998). The price of eggs: Increased investment in egg production reduces the offspring rearing capacity of parents. Proceedings of the Royal Society of London, Series B 265:1731–1735.

Myhre, K., and J. B. Steen (1979). Body temperature and aspects of behavioural temperature regulation in some neonate subarctic and arctic birds. Ornis Scandinavica 10:1–9.

Nisbet, I. C. T. (1973). Courtship-feeding, egg-size and breeding success in Common Terns. Nature 241:141–142.

Nisbet, I. C. (2002). Common Tern (*Sterna hirundo*). In The Birds of North America (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bna.618

Nord, A., and J.-Å. Nilsson (2012). Context-dependent costs of incubation in the Pied Flycatcher. Animal Behaviour 84:427–436.

Ouyang, J. Q., P. J. Sharp, A. Dawson, M. Quetting, and M. Hau (2011). Hormone levels predict individual differences in reproductive success in a passerine bird. Proceedings of the Royal Society B 278:2537–2545.

Pearson, T. H. (1968). The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. Journal of Animal Ecology 37:521–552.

Pienkowski, M. W. (1984). Breeding biology and population dynamics of Ringed Plovers *Charadrius hiaticula* in Britain and Greenland: Nest-predation as a possible factor limiting distribution and timing of breeding. Journal of Zoology 202:83–114.

Pierotti, R. (1981). Male and female parental roles in the Western Gull under different environmental conditions. The Auk 98:532–549.

Quillfeldt, P. (2001). Variation in breeding success in Wilson's Storm Petrels: Influence of environmental factors. Antarctic Science 13:400–409.

Riechert, J., P. H. Becker, and O. Chastel (2014a). Predicting reproductive success from hormone values in the Common Tern (*Sterna hirundo*) while considering food abundance. Oecologia 176:715–727.

Riechert, J., O. Chastel, and P. H. Becker (2012). Why do experienced birds reproduce better? Possible endocrine mechanisms in a long-lived seabird, the Common Tern. General and Comparative Endocrinology 178:391–399.

Riechert, J., O. Chastel, and P. H. Becker (2014b). Regulation of breeding behavior: Do energy-demanding periods induce a change in prolactin or corticosterone baseline levels in the Common Tern (*Sterna hirundo*)? Physiological and Biochemical Zoology 87:420–431.

Romero, L. M., and L. Remage-Healey (2000). Daily and seasonal variation in response to stress in captive Starlings (*Sturnus vulgaris*): Corticosterone. General and Comparative Endocrinology 119:52–59.

Schmid, B., O. Chastel, and L. Jenni (2011). The prolactin response to an acute stressor in relation to parental care and corticosterone in a short-lived bird, the Eurasian Hoopoe. General and Comparative Endocrinology 174:22–29.

Schultner, J., A. S. Kitaysky, G. W. Gabrielsen, S. A. Hatch, and C. Bech (2013a). Differential reproductive responses to stress reveal the role of life-history strategies within a species. Proceedings of the Royal Society B 280:20132090. doi:10.1098/rspb.2013.2090

Schultner, J., A. S. Kitaysky, J. Welcker, and S. Hatch (2013b). Fat or lean: Adjustments of endogenous energy stores to predictable and unpredictable changes in allostatic load. Functional Ecology 27:45–55.

Spée, M., M. Beaulieu, A. Dervaux, O. Chastel, Y. Le Maho, and T. Raclot (2010). Should I stay or should I go? Hormonal control of nest abandonment in a long-lived bird, the Adélie Penguin. Hormones and Behavior 58:762–768.

Spée, M., L. Marchal, D. Lazin, Y. Le Maho, O. Chastel, M. Beaulieu, and T. Raclot (2011). Exogenous corticosterone and nest abandonment: A study in a long-lived bird, the Adélie Penguin. Hormones and Behavior 60:362–370.

Stearns, S. C. (1992). The Evolution of Life Histories. Oxford University Press, Oxford, UK.

Stoleson, S. H., and S. R. Beissinger (1999). Egg viability as a constraint on hatching synchrony at high ambient temperatures. Journal of Animal Ecology 68:951–962.

Sudmann, S. R., P. H. Becker, and H. Wendeln (1994). Sumpfohreule *Asio flammeus* und Waldohreule *A. otus* als Prädatoren in Kolonien der Flussseeschwalbe *Sterna hirundo*. Vogelwelt 115:121–126.

Trivers, R. L. (1972). Parental investment and sexual selection. In Sexual Selection and the Descent of Man: The Darwinian Pivot (B. G. Campbell, Editor). Aldine Publications, Chicago, IL, USA. pp. 136–139.

van der Winden, J. (2005). Nocturnal breeding behavior and related parental investment of the Black Tern. Waterbirds 28:188–192.

Varpe, Ø., T. Tveraa, and I. Folstad (2004). State-dependent parental care in the Antarctic Petrel: Responses to manipulated chick age during early chick rearing. Oikos 106:479–488.

Wang, Q., and J. D. Buntin (1999). The roles of stimuli from young, previous breeding experience, and plasma prolactin in regulating parental behavior in Ring Doves (*Streptopelia risoria*). Hormones and Behavior 35:241–253.

Warnock, N., and L. W. Oring (1996). Nocturnal nest attendance of Killdeers: More than meets the eye. The Auk 113:502–504.

Weidinger, K. (1998). Incubation and brooding rhythm of the Cape Petrel *Daption capense* at Nelson Island, South Shetland Islands, Antarctica. Ibis 140:163–170.

Wendeln, H. (1997). Allocation of parental duties and foraging behavior influence body condition of adult Common Terns, *Sterna hirundo*. Bird Behavior 12:47–54.

Wendeln, H., and P. H. Becker (1996). Body mass change in breeding Common Terns (*Sterna hirundo*). Bird Study 43:85–95.

Wendeln, H., and P. H. Becker (1999a). Effects of parental quality and effort on the reproduction of Common Terns. Journal of Animal Ecology 68:205–214.

Wendeln, H., and P. H. Becker (1999b). Does disturbance by nocturnal predators affect body mass of adult Common Terns? Waterbirds 22:401–410.

Whittingham, L. A., and P. O. Dunn (2001). Male parental care and paternity. Current Ornithology 16:257–298.

Wiggins, D. S. (1989). Consequences of variation in brood size on the allocation of parental care in Common Terns (*Sterna hirundo*). Canadian Journal of Zoology 67:2411–2413.

Wiggins, D. S., and R. D. Morris (1987). Parental care of the Common Tern *Sterna hirundo*. Ibis 129:533–540.

Wingfield, J. C., D. L. Maney, C. W. Breuner, J. D. Jacobs, S. Lynn, M. Ramenofsky, and R. D. Richardson (1998). Ecological bases

of hormone-behavior interactions: The "emergency life history stage." American Zoologist 38:191–206.

Zhang, H., O. Vedder, P. H. Becker, and S. Bouwhuis (2015). Age-dependent trait variation: The relative contribution of within-individual change, selective appearance and disappearance in a long-lived seabird. Journal of Animal Ecology 84:797–807.

APPENDIX

For the analyses presented here, we used a Friedman test to analyze whether the proportion of time when the electronic system was shut down differed according to reproductive phase and time of day. If a significant difference was detected, we used a Wilcoxon test to see which samples differed significantly from each other. Time periods during which the recording system was not running (see Table 1) were mainly caused by switching off the system during the breeding check every other day to move the antennas to new nests. From time to time, some part of the recording system had to be repaired and it was shut down then as well. Additionally, sometimes the system broke down during the night, especially if heavy rainfall occurred. The mean time period with no recording was not affected by breeding phase or time of day (Friedman test: $\chi^2_{3,29} = 6.16$, $P = 0.17$). Detection rate of bird ID by the antenna was much better during the day than at night (Appendix Table 6).

APPENDIX TABLE 6. Comparison of detection of breeding Common Terns on nests by antennas, which recorded bird transponder ID, combined with scales underneath the nest that recorded body weight, in 2 nests over 6 days in northern Germany. Detection rate for males and females (total, day, night) by the antennas as a percentage of the detection rate of the scales is shown, as well as the mean period when terns were absent from the nest (min) during the day and at night for each pair.

Nest ID	Male	Detection (%)		Female	Detection (%)		Absence (min day^{-1})
324	Lancelot	Total	31	Birgit	Total	38	
		Daytime	30		Daytime	45	28.0 ± 10.5
		Nighttime	31		Nighttime	24	2.0 ± 0.4
453	Ernst	Total	55	Salome	Total	38	
		Daytime	55		Daytime	43	16.5 ± 8.6
		Nighttime	56		Nighttime	20	4.0 ± 1.2