

Mothers under stress? Hatching sex ratio in relation to maternal baseline corticosterone in the common tern (*Sterna hirundo*)

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Abstract Sex ratio of progeny should be balanced if costs and benefits of rearing sons and daughters are equal. However, shifts in sex ratio have been demonstrated across bird species and it was suggested that females are able to adjust the primary sex ratio. One possible mechanism is the glucocorticoid corticosterone which rises under stressful conditions and can be deposited into egg yolk by mothers. We analysed primary sex ratio of common terns *Sterna hirundo* from 2006 to 2008 and related it to maternal baseline corticosterone level, laying date and year. Therefore, we took 101 blood samples of 71 breeding females via blood sucking bugs, a method with negligible stress for the birds. Sex ratio did not differ from parity in any of the analysed years, which were characterized by poor food availability and breeding success. Only within 1 year there was a tendency for more females in the last hatched chick. Neither corticosterone level nor laying date or year showed an influence on hatching sex ratio. The negative result concerning primary sex ratio and maternal baseline corticosterone level might suggest conditions to be good enough for mothers to prevent them from depositing high levels of corticosterone into eggs.

Keywords Primary sex ratio · Baseline corticosterone · *Sterna hirundo* · Repeated samples · Hatching position

Introduction

Different factors have been identified that can be linked to offspring sex ratio such as maternal age and condition (Nager et al. 1999), breeding date (Tella et al. 1996), territory quality (Komdeur et al. 1997), or food availability (Appleby et al. 1997). Fisher's theory (1930) predicts a balanced offspring sex ratio at the end of parental care if costs associated with raising sons and daughters are equal and if fitness returns of sexes do not differ for parents. However, in dimorphic species the larger sex, often the male, is assumed to be more costly to rear due to its higher energy demand. In that case and according to Fisher (1930), parents could bias sex ratio of their brood towards the smaller, cheaper sex in order to minimize investment and ultimately increase fitness. Additionally, fitness returns for the sexes could differ and according to Trivers and Willard (1973) parents are predicted to overproduce the sex with the greater reproductive payoff. Especially in polygamous species, high-quality males theoretically have a higher possibility to sire many offspring (Cameron and Linklater 2002), but in many systems females are more likely to reproduce irrespective of their quality (Kruuk et al. 1999; Berkovitch et al. 2000). Even if the population sex ratio is balanced individual females could exhibit a biased brood sex ratio: the probability of producing a son was higher for larger wandering albatross (*Diomedea exulans*) females (Blanchard et al. 2007), and individual Seychelles warblers (*Acrocephalus sechellensis*) produced fewer sons with higher quality territories (Komdeur et al. 1997). Furthermore, females of lesser black-backed gulls (*Larus fuscus*) in worse condition produced more daughters at the end of the laying cycle, whereas supplementary fed mothers did not (Nager et al. 1999).

In a broad range of taxa among birds, a deviation from unity in offspring sex ratio had been demonstrated (Alonso-

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Alvarez 2006; Benito and Gonzáles-Solís 2007). Such a deviation can occur due to sex-biased parental care (Stamps 1990) or different susceptibility of sons and daughters to adverse conditions like starvation (Weatherhead and Teather 1991). In recent years, some studies were suggesting that birds can actively manipulate primary sex ratio of their brood prior to hatching (Pike and Petrie 2003). The mechanisms, however, for such a manipulation largely remain unclear but one possibility is the maternal hormone status around egg production (Pike and Petrie 2006). One of these hormones is corticosterone, the main avian glucocorticoid, which is linked for instance to individual state (body condition: Schoech et al. 1996; Kitaysky et al. 1999, age or experience: Angelier et al. 2007a; Goutte et al. 2010; Riechert et al. 2012) or environmental condition (Romero et al. 2000). Slightly increased baseline levels (by about 50–100 %) are linked to increased foraging effort (Angelier et al. 2007b) and high feeding rate of young (Doody et al. 2008). Furthermore, elevated corticosterone is also related to fitness (Bonier et al. 2009a, b). On the other hand, persistently stressful conditions lead to elevated corticosterone up to the stress level that is about ten times higher (Romero and Romero 2002, Romero and Reed 2005). These above-mentioned effects suggest that corticosterone is a promising trait to link maternal quality, sex-related investment in progeny and maternal fitness (Love et al. 2005).

Maternal hormonal status during egg production is suggested to be reflected in yolk hormones (Hayward and Wingfield 2004). In more detail, if baseline corticosterone is elevated in mothers, e.g. due to poor foraging conditions/poor quality, it could result in a female-biased brood sex ratio (Pike and Petrie 2006; Bonier et al. 2007). Bonier et al. (2007) actually found a steadily increasing female-biased sex ratio with rising baseline corticosterone values. Furthermore, experimentally increased baseline corticosterone in mothers well within the natural range caused a clear bias towards daughters in the brood shortly after the experiment (Love et al. 2005; Pike and Petrie 2006; Bonier et al. 2007). Love et al. (2005) could additionally demonstrate that higher corticosterone in mothers led to increased yolk corticosterone concentration, possibly leading to a female-biased sex ratio. One possibility is that maternal steroids could affect segregation of sex chromosomes during the first meiotic division and thereby influence the sex of the embryo (Pike and Petrie 2003). This provides a mechanism which could possibly adjust sex ratio to the individual condition of a bird because corticosterone rises in birds with low body reserves (Schoech et al. 1996), though Riechert et al. (2012) did not find a connection between corticosterone and body mass in common

terns (*Sterna hirundo*). Sex ratio is biased towards the smaller sex, often daughters, in females with low body mass (Love et al. 2005). On the other hand, females in good condition are able to raise more offspring of the expensive sex, normally sons (Whittingham and Dunn 2000).

Most studies on sex ratio have been conducted on dimorphic or polygamous species where skews occur more often, leading to a bias towards the confirmation of positive results. The aim of this study was to investigate primary sex ratio and a possible relationship of maternal baseline corticosterone level and brood sex ratio in the common tern. This species shows a slightly female-biased sex ratio, which is not significant at hatching (Benito et al. 2013), but in some years significantly female-biased at fledging (Becker et al. 2008). Common terns show a small but significant sexual size dimorphism with sons being up to 6 % larger in head and bill measurements and heavier at fledging (1–3 %) than daughters (Becker and Wink 2002; Gonzáles-Solís et al. 2005). Sons from lighter and younger parents also showed higher post-hatching mortality than daughters (Gonzáles-Solís et al. 2005), together with poorer condition of second chicks in only-male broods compared to mixed broods (Braasch et al. 2011) suggesting that sons could be more vulnerable to adverse conditions. Common terns are genetically monogamous (Gonzáles-Solís et al. 2001). Females start breeding at an earlier age than males (Ludwigs and Becker 2002), tend to produce more young (Ezard et al. 2007) but survival rates of the gender are similar (Ezard et al. 2006), suggesting altogether a slightly higher mean number of female breeding opportunities and higher reproductive output over life. Combined with the small size dimorphism, these circumstances could promote a shift in sex ratio in common terns that indeed was found at fledging by Becker et al. (2008).

Therefore, in a natural, free-living colony we analysed (1) the primary sex ratio over 3 years. Based on the knowledge on common tern biology, however, we did not expect great differences. (2) The effect of hatching position on the proportion of sons in the brood. There is evidence that more females occur in later hatching positions (Nager et al. 1999). (3) The possible relationship between maternal corticosterone and primary sex ratio, taking into account other factors like laying date or year. (4) The change and relationship of brood sex ratio and corticosterone level in individual birds sampled over 2 or 3 years. Based on the literature, we expected to find more daughters in broods produced by mothers with increasing corticosterone. To the best of our knowledge, this is the first study in birds examining corticosterone and sex ratio in the same individuals in consecutive years.

Materials and methods

Study population and field work

The study was carried out between 2006 and 2008 in a common tern colony in the harbour area of Wilhelmshaven, Germany (“Banter See” 53°30′40″N, 8°06′20″E). The colony is situated on six artificial islands (approximately 5 × 11 m), with increasing distance to land. Since 1992 all fledglings were individually marked with a subcutaneously injected microchip (transponder) as well as a metal ring. The passive transponders of marked adults and subadults are automatically registered by special antennas on resting boxes around the colony where birds often settle down (for details see Becker and Wendeln 1997). During the first years (1992–1995), 101 adults were additionally trapped on the nest and fitted with transponders.

All nests were equipped with an antenna for about 1 day during incubation, to record pair mates and assign nest site and breeding success to the individuals. Three times a week the colony was visited; laying dates of new nests were recorded and eggs were marked according to their laying order. Between regular visits we also entered the colony and marked newly laid eggs. As common terns have a laying interval of 1.5–1.9 days (Becker and Ludwigs 2004), we could exactly determine laying position of 254 from 270 eggs. At every following visit in the colony all eggs were checked and immediately after hatching chicks were ringed in their hatching order (first-, second-, and third-hatched chicks were further called a-, b-, and c-chick). As newly hatched chicks sometimes were also ringed between regular visits and as chicks hatch asynchronously, we determined hatching position in 250 of 270 chicks. The c-chick could always clearly be determined, whereas a- and b-chick could not be in eight broods. Laying and hatching order were equivalent in all cases. Since 1998 most of the chicks were sexed using molecular methods (Becker and Wink 2002). During study years 2006–2008, we sexed all chicks of our focal nests by extracting the DNA from some body feathers, which were taken when chicks were fitted with transponders or found dead.

To analyse hatching sex ratio, only clutches where all eggs hatched were included to use the exact primary sex ratio of terns (hatching success in the colony was high, 76 % in 2006, 71 % in 2007 and 82 % in 2008, and in only 9 % of lost eggs the embryo died). This is justified as Benito et al. (2013) at the same colony showed that the hatching sex ratio did not differ between complete and incomplete hatched broods.

Blood sampling

Blood samples of female common terns were taken in the middle of incubation (9–14 days after clutch completion,

5.00–9.00 am). However, from previous work we know that corticosterone does not change from clutch completion to mid-incubation (Riechert et al. unpublished). We used starved third stage larvae of blood-sucking bugs (*Dipetalogaster maximus*) in hollow eggs (Becker et al. 2006; Arnold et al. 2008). 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 (made of artificial resin), one containing the bug (for further detailed information see Becker et al. 2006; Arnold et al. 2008; Riechert et al. 2012). The common tern eggs were kept warm and safe in a box during sampling. During the whole sampling procedure the parent was recorded by the antenna to ensure that we got blood only from the focal bird. After 20–30 min the bugs usually had finished their blood meal and contained about 300 µl of blood. Every year, the bugs successfully sucked blood in more than 80 % of trials. Immediately after the meal, we punctured the bug’s abdomen and extracted the blood by a syringe and stored it in a freezer. The bug method integrating circulating levels and the sampling via needle as a point measure have been successfully validated for baseline corticosterone (Arnold et al. 2008) and prolactin (Riechert et al. 2012).

Hormone assay

Blood samples were centrifuged and the plasma was stored at –20 °C until analysis in the lab. Baseline concentration of corticosterone was measured in the Centre d’Etudes Biologiques de Chizé, France. Total plasma corticosterone was measured in duplicate via radioimmunoassay following procedures described in Lormee et al. (2003). Samples between and within years were partially run in different assays (assay identity had no effect: 2007: $F_{2,15} = 0.291$, $P = 0.751$, 2008: $F_{2,20} = 0.072$, $P = 0.931$). Intra- and inter-assay variation was within a range of 6–11 % ($n = 4$ duplicates for intra-assay variation, measured in known standards). Corticosterone baseline levels (range 1.20–13.60 ng/ml) were comparable to the ones measured in common terns by Heidinger et al. (2006).

Statistical analyses

Deviation from sex ratio 1:1 (sons:daughters) was tested with a two-tailed binomial test. Using ANOVA, we compared mean sex ratio and corticosterone between the years. With an unpaired t test we compared corticosterone between females producing 2- or 3-egg clutches. For all these tests we used a subset of data where every individual occurred only once (random selection).

In mothers, we examined the factors influencing hatching sex ratio by fitting a generalized linear model with a

binomial error structure and logit link function. The number of sons in a brood was used as the response variable and clutch size was the binomial denominator. Since we had 1–3 measures per individual, the idcode was used as subject and sample as repeated measure. We tested for effects of the factor year as well as the covariate corticosterone and their two-way interactions on hatching sex ratio. We used the information-theoretic approach to identify suitable models to predict primary sex ratio (Burnham and Anderson 2002). We used the Akaike information criterion (AIC) and calculated ΔAIC and Akaike weight (W_i) to determine the most suitable models. The model with the lowest AIC was considered to be the best one; models with a ΔAIC of <2 to the best model were suggested to have substantial support in the data.

With a Pearson correlation we investigated the relationship between the change in corticosterone and in sex ratio between years in repeatedly sampled individuals. Additionally, the change in sex ratio and baseline corticosterone from 1 year to the next was analysed by building the ratio (increase/decrease) in the two variables and relating them.

All statistical analyses were two-tailed, means were expressed as mean \pm 1SE, and level of significance was set to $P < 0.05$. All analyses were performed with SPSS 17.

Results

The sampled broods contained around 50 % sons (Table 1). We found neither a significant difference in sex ratio between the 3 years ($F_{2,68} = 0.929$, $P = 0.400$) nor in corticosterone baseline levels ($F_{2,68} = 0.724$, $P = 0.498$), and in none of the years sex ratio differed from parity (Table 1, binomial test: 2006: $P = 0.905$; 2007: $P = 0.659$; 2008: $P = 0.182$; in total: $P = 0.713$, $n = 184$ chicks). Furthermore, neither in 2- nor in 3-egg clutches sex ratio differed from the expected 50 % for each sex (binomial test: 2-eggs: $P = 0.237$, 41.4 % sons, $n = 58$ chicks; 3-eggs: $P = 0.181$, 56.4 % sons, $n = 126$ chicks).

Table 1 Mean brood sex ratio, corticosterone value and sex ratio for the first, second and third hatched chick (a, b, c) among analysed years

	2006	2007	2008
Sex ratio	51.6 \pm 6.9 (70)	54.7 \pm 7.8 (46)	42.0 \pm 6.0 (68)
a-chick	53.3 \pm 9.3 (30)	55.6 \pm 12.1 (18)	56.5 \pm 10.6 (23)
b-chick	53.3 \pm 9.3 (30)	44.4 \pm 12.1 (18)	39.1 \pm 10.4 (23)
c-chick	40.0 \pm 10.3 (10)	70.0 \pm 15.3 (10)	27.3 \pm 9.7 (22)
Corticosterone	6.22 \pm 0.5 (30)	5.74 \pm 1.1 (18)	5.16 \pm 0.42 (23)

Values are expressed as mean \pm 1SE, sample size N in brackets (chicks for sex ratio and females for corticosterone)

The proportion of sons in the first, second and third chick (a-chick, b-chick, c-chick) was not significantly different from 50:50 in any case (a: $P = 0.477$; b: $P = 0.635$; c: $P = 0.280$, Table 1). In 2006 and 2007 we found no indication for a biased sex ratio in relation to hatching position (Table 1, $P > 0.3$ in all cases). However, in 2008 when the proportion of sons was lowest among the 3 years, terns tended to produce more daughters among the last hatched chick (Table 1, a-chick, b-chick: $P > 0.4$, respectively, c-chick: $P = 0.052$). Model selection procedure indicated that the best model explaining brood sex ratio contained year, corticosterone and their interaction term (Table 2; Fig. 1 for the relationship between baseline corticosterone and offspring sex ratio). This model was about four times better in explaining hatching sex ratio than the next one (Table 2, W_i). However, no factor significantly influenced primary sex ratio of terns ($P > 0.05$ in every case). In repeatedly sampled individuals the change in baseline corticosterone from one year to the next was not significantly correlated to the change in sex ratio (2006–2007: $r = 0.371$, $P = 0.235$, $N = 12$; 2007–2008: $r = -0.163$, $P = 0.594$, $N = 13$). Additionally, the proportional increases or decreases in baseline corticosterone and sex ratio between years were not significantly correlated (2006–2007: cort: mean increase by 1.54 times, sex ratio: mean decrease by 1.61 times, $r = 0.035$, $P = 0.914$, $N = 12$; 2007–2008: cort: mean increase by 0.07 times, sex ratio: mean increase by 0.1 times $r = 0.329$, $P = 0.273$, $N = 13$).

Discussion

Contrary to most other studies, we took blood samples in mid-incubation and not around egg production. If corticosterone levels change during the period of incubation, this would explain the missing link between corticosterone concentration and brood sex ratio. However, our results indicate that corticosterone shortly after clutch completion in females did not differ from levels in the same birds measured during mid-incubation (Riechert et al. unpublished).

Table 2 Outcome of the GEE analysing the effect of different variables and interaction terms on hatching sex ratio (proportion of sons) in common terns

Variables in the model	AIC	ΔAIC	W_i
Year, cort, year*cort	310.367	0	0.731
Year	313.082	2.715	0.188
Year, cort	315.605	5.238	0.053
Intercept	317.591	7.224	0.020
Cort	320.122	9.755	0.006
Year*cort	321.756	11.389	0.002

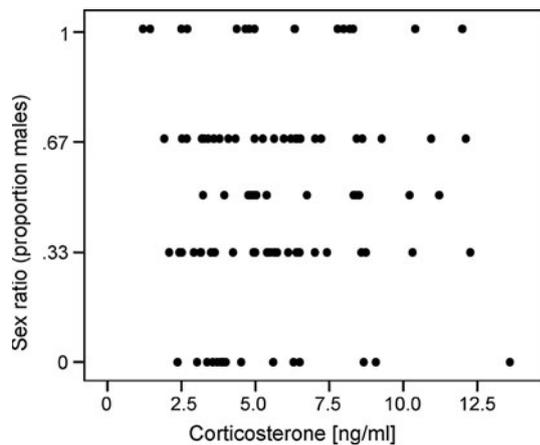


Fig. 1 Relationship between maternal baseline corticosterone level and primary offspring sex ratio (proportion of males) in common terns (R^2 linear = 0.008)

Hatching sex ratio in our sampled broods in all 3 years was comparable to sex ratio determined in the whole common tern colony (Benito et al. 2013). Neither in the entire sample of broods nor in the particular years did the proportion of sons and daughters differ significantly. Only in 2008, we found a marginal shift towards daughters which was due to more daughters in the second and mainly the third hatching position. In contrast, Szczys et al. (2001) showed a female-biased sex ratio in roseate terns (*Sterna dougallii*) only in the first hatched chick. As it was shown for black-headed gulls *Larus ridibundus* (Müller et al. 2005), female common terns are more likely to survive to fledging than males (Fletcher and Hamer 2004; González-Solís et al. 2005) and the overall breeding success in the whole colony was slightly higher in 2008 compared to previous years (Dänhardt and Becker 2011; Szostek and Becker 2012). In most years, chicks in the second and particularly the third hatching position have low chances to survive to fledging due to asynchronous hatching (e.g. Becker and Fink 1985) and to the resulting benefit in growth and competition for food of first hatched chicks. Perhaps terns can improve their success particularly in better years if the second and/or third chick is a daughter (Becker and Wink 2003; Braasch et al. 2011).

Our results showed no influence of maternal baseline corticosterone level on primary sex ratio of common terns. In contrast, other studies found a clearly female-biased hatching sex ratio with increasing corticosterone level of the mother (Pike and Petrie 2006; Bonier et al. 2007). An elevated glucocorticoid level in mothers can induce a transfer of corticosterone to egg yolk which could lead to a more female-biased sex ratio (Petrie et al. 2001; Love et al. 2005). It is possible that baseline corticosterone values of the terns did not reach levels high enough to affect sex ratio of progeny. This could indicate that stress in female

common terns was not high enough to lead to a considerable increase in corticosterone concentration among eggs, despite comparably bad breeding conditions in all analysed years (Szostek and Becker 2012) and higher baseline corticosterone than in following years with better food availability (Riechert et al. unpublished). It is also possible that in terns higher corticosterone levels do not affect sex ratio in the same way as it was found in other species. Therefore, further studies are needed to test whether increased corticosterone levels can lead to a shift in sex ratio of common terns or not.

Benito and González-Solís (2007) showed a general tendency for dimorphic species to bias their sex ratio towards the smaller, cheaper sex. This leads to another possible explanation for the missing relation of hatching sex ratio and corticosterone: common terns are quite monomorphic, with sons being slightly larger and heavier than daughters (Becker and Wink 2002) implying higher costs for parents to raise sons successfully. However, compared to other species with up to 20 or 30 % larger males, female common terns can possibly not reduce their investment in offspring significantly by producing mainly daughters, offering no benefit of a major shift in sex ratio particularly under stressful conditions.

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