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Physiological and fitness correlates of experimentally altered hatching asynchrony magnitude in chicks of a wild seabird

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ABSTRACT

Nest-bound chicks depend entirely on their parents for food, often leading to high sibling competition. Asynchronous hatching, resulting from the onset of incubation before clutch completion, facilitates the establishment of within-nest hierarchy, with younger chicks being subject to lower feeding and growth rates. Because social and nutritional stresses affect baseline stress hormone levels in birds, younger chicks are expected to have higher levels of corticosterone than their siblings. As previous studies showed that hatching asynchrony magnitude influences the course of sibling competition, it should also affect baseline corticosterone. We measured baseline corticosterone at age 5 days in nestling black-legged kittiwakes (*Rissa tridactyla*) in 3 types of experimental broods: synchronous, asynchronous, and highly asynchronous. Sexual dimorphism takes place during chick-rearing and might also influence baseline corticosterone, we thus included chick sex in our analyses and also monitored chick growth and survival. Baseline corticosterone did not differ among A-chicks, but was higher in B-chicks from highly asynchronous broods compared with the other brood types, in line with the presumed increase in nutritional stress. In asynchronous broods, A-chicks had higher baseline corticosterone than their siblings, contrary to our expectations. We interpret that result as a cost of dominance among A-chicks. In line with previous studies, mass gain was negatively correlated with baseline corticosterone levels. We found that baseline corticosterone predicted survival in a sex-specific way. Regardless of hatching rank, males with higher baseline corticosterone suffered higher mortality, suggesting that males were more sensitive to high level of stress, independently of its cause.

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1. Introduction

Environmental changes, such as social or nutritional challenges, can influence baseline stress hormone levels (i.e., glucocorticoids) and might also influence fitness. However, the relationships between these three variables are not clear yet (Bonier et al., 2009). Stressors such as reduced food availability (Kitaysky et al., 1999b), a change of mate (Angelier et al., 2007), mate incompatibility (Griffith et al., 2011) or any change in the social environment (Pryke et al., 2007) can lead to increased baseline levels of stress hormones and potentially to lower fitness. However, Chastel et al. (2005), for example, showed that chick-rearing black-legged kittiwakes (*Rissa tridactyla*) have higher levels of corticosterone (the major stress hormone in birds) than failed breeders, which probably triggers an increase in foraging activity that compensates for the energetic costs of chick rearing (Golet et al., 2000, 1998), therefore increasing fitness.

Similarly, chicks are exposed to social and nutritional stresses which could differentially affect baseline corticosterone levels. Chicks from altricial and semi-precocial species are nest-bound, substantially developing after hatching and dependent on parental food provisioning (Starck and Ricklefs, 1998). In polytocous species, food shortage typically leads to sibling competition and potentially to the unequal allocation of food between chicks (Mock and Parker, 1997). That outcome is especially common when hatching asynchrony, resulting from the onset of incubation before clutch completion, leads to the establishment of a within-brood hierarchy (Magrath, 1990). The older chick's size advantage allows

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it to dominate through begging and/or overt aggression toward its siblings, thereby receiving a disproportionate share of food from the parents (Cotton et al., 1999; Mock and Parker, 1997). Facing reduced feeding rates and growth (e.g., Gilby et al., 2011; Hébert, 1993) and a greater likelihood of starvation (Drummond et al., 1986; Hébert, 1993), younger chicks are expected to have higher baseline levels of corticosterone than their older siblings. While some studies have confirmed those expectations (e.g., Eraud et al., 2008; Nuñez-de la Mora et al., 1996; Tarlow et al., 2001), others have found no effect of rank on baseline corticosterone (e.g., Blas et al., 2005; Poisbleau et al., 2010; Ramos-Fernandez et al., 2000) or even the reverse pattern. The latter results (Love et al., 2003; Schwabl, 1999) occurred in captive populations, with scramble competition within the brood mediated via begging.

Beyond simple hatching order, the magnitude of hatching asynchrony influences sibling competition (Gilby et al., 2011; Mock and Ploger, 1987; Osorno and Drummond, 1995), and may affect social and nutritional stress levels among chicks (Love and Williams, 2008a; Love et al., 2003; Merkling et al., 2013). Several studies in species competing via begging or via overt aggression found that synchronous (simultaneous) hatching, led to an unstable hierarchy and an increase of sibling competition through an escalated conflict, with comparatively equal feeding and growth rates among chicks (Gilby et al., 2011; Mock and Ploger, 1987; Osorno and Drummond, 1995). Thus, in synchronous broods, all chicks are expected to show equal levels of baseline corticosterone. Conversely, increasing hatching asynchrony magnitude experimentally further disadvantages a younger chick, which is heavily attacked and more rarely fed, is growing slowly and is more likely to die than in naturally asynchronous broods (e.g., Love et al., 2003; Mock and Ploger, 1987; Osorno and Drummond, 1995). The social and nutritional stress of being subordinate should thus increase with greater hatching asynchrony, and younger chicks should exhibit higher baseline corticosterone levels than in the natural situation (but see Love et al. (2003)). The response in older siblings, however, would not change necessarily.

To our knowledge, no study has investigated in a wild bird population the effect of hatching asynchrony magnitude on baseline corticosterone levels. We studied this relationship in black-legged kittiwakes (*R. tridactyla*), a seabird usually having 2 chicks hatched asynchronously (mean: 1.35 days apart in our study population, Gill et al., 2002). We showed recently that experimental manipulation of hatching asynchrony magnitude influences the course of sibling competition (Merkling et al., 2013). In synchronous broods, both chicks behaved almost identically and had similar growth rates, whereas greater hatching asynchrony led to increased attacks on B-chicks (i.e., second-hatched chicks), with higher begging intensity and reduced growth and survival prospects in that group. Here, our aim was to investigate how baseline corticosterone levels vary with birth rank and magnitude of hatching asynchrony among chicks of this same experiment (Merkling et al., 2013). We assessed baseline corticosterone levels when chicks were 5 days of age. We chose this age because nutritional and social stresses endured by B-chicks are known to be high at this stage (Merkling et al., 2013). Males, which grow faster and reach a larger size than females near fledging (Merkling et al., 2012), are expected to be more sensitive to social and nutritional stresses. We therefore included chick sex in our analyses. We predicted that synchronous hatching would lead to equal baseline corticosterone levels in A and B-chicks (with higher levels in males), whereas differences between siblings would increase with increasing hatching asynchrony magnitude. Asynchronously hatched B-chicks, especially males, should have higher baseline corticosterone levels than A-chicks.

Additionally, we explored relationships among body condition, growth patterns, hatching asynchrony magnitude, rank and baseline corticosterone levels. We expected a negative correlation between chick body condition and/or growth and baseline corticosterone (e.g., Eraud et al., 2008; Kitaysky et al., 1999a; Müller et al., 2010; Rensel et al., 2011; Sockman and Schwabl, 2001). Finally, we predicted that high baseline corticosterone levels (i.e., in chicks experiencing high social and nutritional stress) would be associated with low survival (Blas et al., 2007) upon controlling for rank, chick sex, sibling sex, and hatching asynchrony magnitude.

2. Materials and methods

2.1. Study site

The study was conducted from mid-May to mid-August 2011 in a population of black-legged kittiwakes nesting on an abandoned U.S. Air Force radar tower on Middleton Island (59° 26′N, 146° 20′W), Gulf of Alaska. The tower is a 12-walled polygon with artificial nest sites that have been added to the upper walls, which allowed us to monitor easily the breeding adults and their chicks from inside the building (for more details, see Gill and Hatch (2002)). Nests were checked twice daily (9:00 and 18:00) throughout the breeding season to document events such as laying, hatching, and chick mortality.

2.2. Experimental design

Each egg (2 being the typical clutch size in this population) was individually marked (A and B for the first- and second-laid egg, respectively) with non-toxic waterproof ink within 12 h of laying. 24 days after laying (i.e., 3 days before the expected hatching date: Hatch et al., 2009), eggs from 2-egg clutches ($N = 307$) were placed in an incubator (Compact S 84 MP GTFS, Grumbach Brutgeraete GmbH, Asslar, Germany, set at 37.4 °C and 63% of humidity) to control for hatching time. They were replaced in the nests by hen eggs of similar size that had been warmed in the incubator and artificially marked to mimic the natural temperature and pigmentation of kittiwake eggs. Parental incubation resumed immediately after the surrogate eggs were placed.

Hatching occurred in the incubator and its timing was assessed to the nearest 2 h between 6:00 and 22:00 and to the nearest 6 h at night. Chicks were marked on the head with a non-toxic marker to identify their original rank. We then weighed each chick to the nearest 0.1 g with an electronic scale, measured head-bill and tarsus lengths to the nearest 0.1 mm with a calliper and measured wing length to the nearest 1 mm with a wing ruler. Each chick was also blood sampled for molecular sexing from the brachial vein (~50 μl) using a sterile 25 gauge needle and a capillary tube (for a detailed molecular sexing protocol see Merkling et al. (2012)). Samples were kept in Longmire buffer (Longmire et al., 1988) and stored at −20 °C until analysis. No sex ratio bias was found in relation to hatching order (44 females and 30 males among A-chicks, 33 females and 40 males among B-chicks, $\chi^2_1 = 2.44$, $P = 0.12$).

To control for parental effects, we put each chick in a foster nest just after hatching, creating broods consisting of an A-chick (born from a first-laid egg) and an unrelated B-chick (born from a second-laid egg). By choosing chicks according to their hatching date, we experimentally created 3 types of broods with different magnitudes of hatching asynchrony. The first type contained 2 chicks hatched less than 1 day apart (mean ± SE: 0.28 ± 0.05 days, $N = 31$, hereafter called 'synchronous broods'), the second contained 2 chicks hatched between 1 and 2 days apart (1.48 ± 0.07 days, $N = 26$, hereafter called 'asynchronous broods'), while the third contained 2 chicks hatched more than 2 days apart (2.31 ± 0.07 days, $N = 26$, hereafter called 'highly asynchronous

broods'). The A-chick was always put first in the nest and stayed alone until the B-chick hatched in the incubator and was then put back into the nest. The mean natural hatching interval (for pairs that had their 2 eggs hatched in the incubator) was 1.64 days (SE ± 0.07 days, $N = 117$), which is slightly higher than previously reported in the same colony: 1.35 ± 0.09 days (Gill et al., 2002). Our experimental manipulation thus encompassed the mean natural hatching interval and entailed a wide, but biologically plausible, range around it. Previous analyses of behavioural data on those same chicks revealed that within-brood hierarchy is established early in chick development and more easily when hatching asynchrony magnitude is high (Merkling et al., 2013). It is to be noticed that when analysing behavioural data, we considered hatching asynchrony magnitude as a continuous variable, whereas here we considered it as a categorical variable for clarity purposes.

When each chick was 5 days of age we took a blood sample within 3 min of capture to determine their baseline corticosterone level (Romero and Reed, 2005). We wanted to assess baseline corticosterone levels at a stage when nutritional and social stresses might be high for B-chicks. In kittiwakes, chick aggression decreases with age (i.e., the hierarchy takes place within a few days) and B-chicks in asynchronous broods mainly suffer in terms of growth and survival early in their life (Merkling et al., 2013). Hence, the age of 5 days seemed an appropriate age to investigate the influence of hatching asynchrony magnitude on baseline corticosterone levels. Blood samples were collected from the alar vein with a 21-gauge needle and capillary tubes (maximum volume collected: 225 μl). Sampling occurred between 11:00 and 16:00 to minimise the effect of diurnal fluctuations on plasma corticosterone levels (Breuner et al., 1999; Romero and Remage-Healey, 2000; Tarlow et al., 2003).

2.3. Chick growth

Chicks weights and measures were taken every 5 days from day 5 to day 35 (i.e., close to fledging: Hatch et al., 2009). Measurements were the same as at hatching (see Section 2.2). We ran a principal component analysis on wing, tarsus and head-bill lengths on all ages and considered the score of each individual on the first principal component (94% of total variance explained) as a measure of its structural size at a given age (e.g., Blanchard et al., 2007). We calculated mass gain and growth in structural size between 0 and 10 days, by estimating the slope of the linear regression between body mass and age and between structural size and age, respectively. We also estimated chick body condition at the stage when corticosterone levels were assessed (i.e., at day 5) by calculating residuals of the linear regression between chick mass and structural size on that day.

2.4. Corticosterone assays

All hormonal analyses were performed at the Centre d'Etudes Biologiques de Chizé. Plasma concentrations of corticosterone were determined in one assay following methods described in Lormée et al. (2003). The detection limit was 0.3 ng/mL, and the intra-assay coefficient of variation was 6% ($n = 5$ duplicates). We chose not to assess free corticosterone and corticosteroid-binding globulin concentrations on the premise that total corticosterone concentration is the more biologically relevant estimate of corticosterone levels (Schoech et al., 2013). Baseline corticosterone levels were assessed for 150 chicks for which we had information on sex and sibling sex, but 3 outliers were removed from statistical analyses because their corticosterone concentrations were above 20 ng/ml (i.e., above baseline corticosterone levels found in kittiwake chicks in other studies, Kitaysky et al., 2001b). We speculate that in those chicks the stress response had already begun, because sampling time was close to 3 min (Romero and Reed, 2005) or because they were otherwise stressed in the nest before we captured them. Corticosterone levels were considered to reflect the baseline level in all remaining chicks ($N = 147$) (Chastel et al., 2005) and statistical results were unaffected if the 3 outliers were included.

2.5. Statistical analyses

For each analysis, we started with a complete model and successively removed each term beginning with the terms of the highest degree. We compared the change in deviance after removal of a term using a χ^2 test for linear mixed models (LMM) and Cox models. When an interaction was tested, the corresponding main effects were kept in the model.

To meet model assumptions (normality of data and residuals and homoscedasticity), baseline corticosterone levels ($\lambda = 0.35$) were transformed using the Box–Cox transformation (Box and Cox, 1964) in the *MASS* package (Venables and Ripley, 2002). As some chicks died before 10 days and we were thus unable to calculate their mass gain, structural size growth rate or body condition, we ran a first set of models without the growth variables. The starting model was complete and contained rank, hatching asynchrony, sex, sibling sex, and all two-way and three-way interactions containing rank, with nest as a random effect to account for the non-independence of chicks within a nest. When considering the growth variables (i.e., a second set of models), we removed sex and sibling sex from the models because they did not seem to affect baseline corticosterone levels (see Section 3.1) and because remaining sample sizes were too small ($N = 138$). As structural size growth rate, mass gain and body condition were inter-correlated (Spearman correlation: all $p < 0.01$), we did not consider them in the same model, but ran three sets of models within this second set of models. In each of them the starting model was complete and contained the interactions between rank, hatching asynchrony, and the growth/condition variable. For models with structural size growth rate, presented results exclude three outliers with very low growth rates, but considering them led to similar results.

For survival analyses ($N = 147$), we used mixed effects Cox proportional hazards models (i.e., frailty models) in the *coxme* package (Therneau, 2012) with nest as a random effect. We started with a complete model including three-way interactions in addition to the main effects—baseline corticosterone levels, rank, hatching asynchrony, sex, and sibling sex.

All analyses were conducted with R 2.14.2 (R Development Core Team, 2012). Results are shown with mean ± standard error (SE).

3. Results

3.1. Effects of hatching asynchrony, rank, sex and sibling sex on chick corticosterone levels

Baseline corticosterone levels were significantly affected by the interaction between rank and hatching asynchrony ($\chi^2_2 = 6.11$, $p = 0.047$, Fig. 1). In order to interpret this interaction, we did pairwise comparisons of rank effects within hatching asynchrony classes as well as of hatching asynchrony classes within rank and corrected for multiple comparisons using the sequential Bonferroni procedure (Holm, 1979). Nevertheless, due to a lack of statistical power, none of the pairwise comparisons were significant after correction (all $p > 0.2$). To reveal differences and to better interpret this interaction, we created a greater contrast between hatching asynchrony classes by removing nests with hatching asynchrony magnitude close to class edges (1 ± 0.1 and 2 ± 0.1 days ($N = 29$)). The same interaction was then more pronounced ($\chi^2_2 = 8.18$,

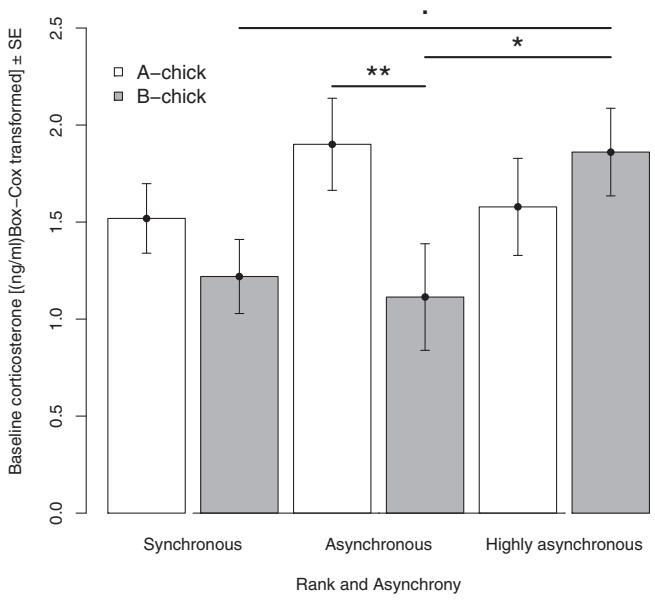

Fig. 1. Baseline corticosterone levels (mean ± SE; Box–Cox transformed ng/ml) according to rank and hatching asynchrony. White bars represent A-chicks; grey bars represent B-chicks. Significant ($p < 0.05$) and marginally significant ($p < 0.1$) pairwise comparisons (with post hoc Bonferroni correction for multiple comparisons) are indicated by asterisks and points, respectively. The degree of significance was assessed from a dataset comprising the greatest contrast between hatching asynchrony classes (see Section 3.1 for explanations).

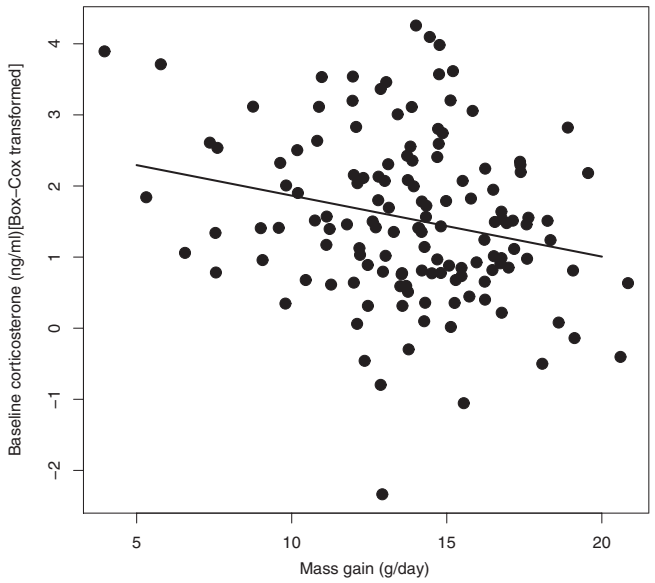

Fig. 2. Correlation between baseline corticosterone levels (Box–Cox transformed ng/ml) and mass gain (g/day) during the first 10 days. Dots represent data points and the fitted line is the predicted linear model.

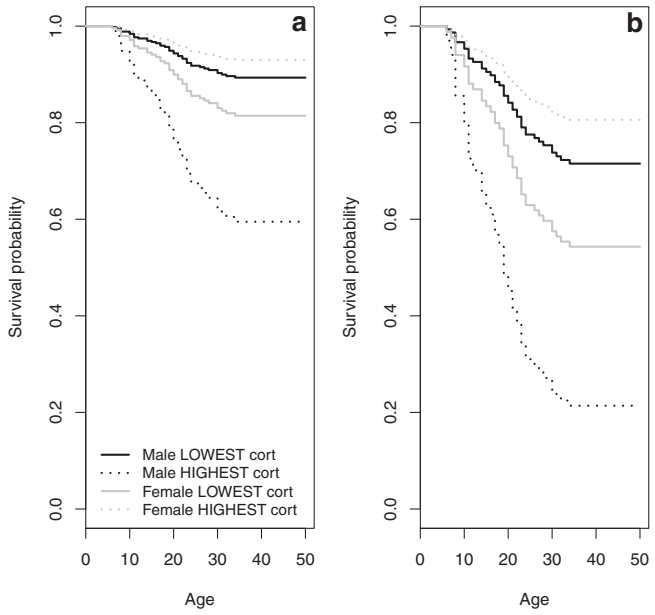

Fig. 3. Chick survival probability according to baseline corticosterone levels (solid lines: lowest baseline corticosterone [1 ng/ml]; dotted lines: highest baseline corticosterone [10 ng/ml]) and chick sex (black lines: males; grey lines: females) for (a) A-chicks and (b) B-chicks. Although baseline corticosterone levels were analysed as a continuous variable (see Section 3.3), on the figure, we chose to focus on the lowest and the highest value for illustrative purposes.

$p = 0.017$). Multiple comparisons revealed that B-chicks in asynchronous broods had significantly lower baseline corticosterone levels than their sibling in the same broods (before correction: $p = 0.001$; after correction: $p = 0.009$; Fig. 1). Moreover, there were no differences across treatments for A-chicks (all $p > 0.8$). Among B-chicks, baseline corticosterone levels were higher in highly asynchronous broods than in synchronous and asynchronous broods, however not significantly in the first case (before correction: $p = 0.013$ and $p = 0.001$, respectively; after correction: $p = 0.091$ and $p = 0.01$, respectively; Fig. 1). Neither chick sex, sibling sex or their interactions with hatching asynchrony magnitude or rank was significant (all $p > 0.15$). No significant sex ratio bias in relation to hatching asynchrony magnitude and rank was found ($\chi^2_6 = 2.92$, $p = 0.82$) suggesting that our manipulations were not biased in relation to chick sex.

3.2. Corticosterone levels and growth/condition variables

Mass gain was negatively correlated with baseline corticosterone levels ($\chi^2_1 = 8.90$, $p = 0.0028$, Fig. 2), while the negative correlation between structural size growth rate and baseline corticosterone levels was only marginally significant ($\chi^2_1 = 2.91$, $p = 0.088$). We found no correlation between chick body condition and baseline corticosterone levels. Apart from the interaction between rank and hatching asynchrony magnitude (see Section 3.1), none of the other interactions (growth variable * rank or growth variable * hatching asynchrony) were significant (all $p > 0.30$).

3.3. Corticosterone levels, chick sex, sibling sex, egg rank and survival

Chick survival was related to the interaction between baseline corticosterone levels and chick sex, regardless of rank ($\chi^2_1 = 5.32$, $p = 0.021$, Fig. 3). Among males, the negative relationship between survival and baseline corticosterone was very close to significance (Cox model: $\chi^2_1 = 3.79$, $p = 0.051$, Fig. 3), whereas no similar relationship was detected among females (Cox model: $\chi^2_1 = 1.74$, $p = 0.19$, Fig. 3). A-chicks had higher survival than B-chicks ($\chi^2_1 = 9.27$, $p = 0.002$, Fig. 3) and chicks with a female sibling tended to be more likely to die than those with a male sibling ($\chi^2_1 = 3.71$, $p = 0.054$).

4. Discussions

4.1. Effects of hatching asynchrony, rank, sex and sibling sex on chick corticosterone levels

This is the first experimental investigation of the links between hatching asynchrony magnitude and chick baseline

corticosterone in a wild population. The observed pattern depended on chick rank in the brood. Only in B-chicks did the magnitude of hatching asynchrony affect baseline corticosterone levels. Corticosterone was significantly higher in B-chicks from highly asynchronous broods than from the other types of brood. This is consistent with previous findings reporting higher social and nutritional stress for B-chicks in highly asynchronous broods, where they were heavily attacked, grew more slowly, and were less likely to fledge (Osorno and Drummond, 1995; Merkling et al., 2013). In our study, B-chicks of highly asynchronous broods were also significantly more likely to beg than in other brood types, probably signalling their higher hunger level (Merkling et al., 2013). Their higher baseline corticosterone levels might thus have facilitated their higher begging rates (Kitaysky et al., 2001b). However, contrary to our predictions and despite slower growth and more attacks received (Merkling et al., 2013); B-chicks in asynchronous broods (i.e., close to the natural situation) did not have lower baseline corticosterone levels than B-chicks in synchronous broods. Our results differ from those in a captive population of American kestrels (*Falco sparverius*), where authors investigated the role of hatching asynchrony magnitude on corticosterone levels (Love et al., 2003). In that study, increased hatching asynchrony led to increasing baseline corticosterone levels among older but not younger chicks, contrary to what we found. Parents were fed *ad libitum* in the kestrel study and chicks did not attack each other. Therefore, younger chicks probably did not endure the same social and nutritional stresses as in our study, which might explain the different impact of rank for large hatching asynchrony especially.

Surprisingly and contrary to our predictions, A-chicks in asynchronous broods (i.e., approximating the natural situation) had significantly higher baseline corticosterone levels than their siblings (see also Love et al. (2003)). It is unlikely that differences in baseline corticosterone levels in asynchronous broods came from differences in yolk corticosterone, as A- and B-egg yolk corticosterone contents were found not to differ in black-legged kittiwakes (Vallarino et al., 2012). A previous study on kittiwakes found no differences between A- and B-chicks' baseline corticosterone levels in natural broods. However, chicks in that study were 12–15 days old (i.e., after most of chick mortality occurred), which may have biased patterns (Brewer et al., 2010). Sockman and Schwabl (2001) found that yolk androgens can influence neuroendocrine development and lead to higher plasma baseline corticosterone levels in chicks. In kittiwakes, B-eggs have higher concentrations of androgens than A-eggs (Müller et al., 2012; Vallarino et al., 2012). We would thus expect B-chicks to exhibit higher corticosterone levels, in line with our prediction, but we found the contrary. Our result could be viewed as a cost of being dominant for A-chicks in asynchronous broods as this was reported in cooperative breeders, where it was considered as a cost of dominance (Gesquiere et al., 2011). However, the pattern seems inconsistent in birds (reviewed by Creel (2001)). In kittiwakes, A-chicks are highly aggressive during the first several days after hatching, when their dominance is established (Braun and Hunt, 1983; Leclaire et al., 2011; White et al., 2010). Comparable to the situation in cooperative breeders perhaps, this may be stressful for A-chicks, providing an explanation for the discrepancy between our prediction and results. Accordingly, baseline corticosterone levels were the lowest for A-chicks in synchronous broods (i.e., where there was no hierarchy), albeit not significantly so.

Altogether, our results suggest stress associated with dominance in A-chicks when a hierarchy is established and substantial stress from being subordinate in B-chicks only when heavily attacked and growing very slowly. Contrary to our predictions, chick sex seemed not to influence baseline corticosterone levels, either alone or in interaction with hatching asynchrony magnitude, probably because chick sex has low influence on growth at 5 days of age (Merkling et al., 2012).

4.2. Corticosterone levels and growth/condition variables

We found no correlations between chick body condition and baseline corticosterone levels regardless of rank (see also Love and Williams (2008a)), contrary to previous studies that often report that chicks in a lower nutritional state (i.e., in poor condition) exhibit higher baseline corticosterone levels (e.g., Eraud et al., 2008; Kitaysky et al., 1999a; Müller et al., 2010; Sockman and Schwabl, 2001). However, prior studies used different means of estimating chick body condition (e.g., body lipids: Kitaysky et al., 1999a; furcula fat score: Müller et al., 2010). This may explain why we found no correlation with our body condition index (i.e., residuals of the linear regression between mass and structural size) despite correlations with mass gain and structural size—those two variables might have better represented chick "condition" in this study. Chicks gaining less weight and growing slowly during the first 10 days had higher baseline corticosterone levels, regardless of hatching asynchrony magnitude. Their higher baseline corticosterone levels may indicate nutritional stress caused by lower feeding rates or lower-energy food (Kitaysky et al., 2001a) and may have facilitated food-begging (Kitaysky et al., 2001a).

4.3. Corticosterone levels, chick sex, sibling sex, egg rank and survival

Although chick sex did not influence baseline corticosterone, survival probability depended significantly on the interaction between sex and corticosterone. Regardless of rank, males with higher baseline corticosterone were less likely to survive than males with lower corticosterone, while baseline corticosterone was not correlated with females' survival prospects. We found previously that male chicks grow faster and reach a larger size near fledging than females (Merkling et al., 2012), and presumably have higher energy requirements (our unpublished data), as found in other species (Cameron-MacMillan et al., 2007; Clutton-Brock et al., 1985; but see Torres and Drummond, 1999). However, survival probability did not depend on the interaction between chick sex and mass gain (our unpublished data): the higher mortality of males with high baseline corticosterone seemed independent of their growth. Our results suggest that male survival is relatively sensitive to stress, irrespective of its cause. Interestingly, Goutte et al. (2010) found that adult male kittiwakes with a corticosterone implant were less likely to survive during the next 2 years as compared to control birds. The authors did not measure females, however, and the corticosterone implants produced a higher corticosterone concentration than the baseline level measured here.

Many studies have investigated, in sexually dimorphic species, whether the viability of the larger sex is more sensitive to poor conditions during early life (e.g., Kalmbach et al., 2005; Love and Williams, 2008b; Nager et al., 2000), but meta-analyses suggest that the pattern is inconsistent (Jones et al., 2009; Raberg et al., 2005). Here, we found no evidence that subordinate males were more likely to die than dominant males, as suggested by the absence of interaction between sex and rank. Hence, our results do not support the idea that the larger sex is more sensitive to poor environmental conditions. However, the lower survival of males with high baseline corticosterone levels could partly be explained by higher yolk corticosterone levels that have been shown to negatively affect male development and survival in European starlings (Love and Williams, 2008b; Love et al., 2005).

5. Conclusions

Our data show that experimentally increased hatching asynchrony magnitude influences baseline corticosterone in B-chicks, but not in A-chicks. We interpret the observed rise of corticosterone levels in highly-asynchronous B-chicks as an indication of nutritional stress. Contrary to our predictions, however, A-chicks in asynchronous broods (i.e., similar to the natural situation) had higher baseline corticosterone levels than B-chicks—a possible cost of being aggressively dominant, as found in some cooperatively breeding species. This hypothesis should be tested in other siblicidal species and under additional controls, where for example the same chicks are alternatively in dominant and subordinate positions. Regardless of rank, male survival probability was negatively correlated with high baseline corticosterone early in life. Slow growth did not affect male survival more than female survival, which therefore suggests that our result is not a consequence of higher male sensitivity to poor conditions early in life, as suggested by previous studies (Kalmbach et al., 2005; Nager et al., 2000), but rather a consequence of higher male sensitivity to stress, which could arise simply from sexual dimorphism. Measuring sex-specific stress-induced corticosterone in different developmental stress conditions (Love and Williams, 2008a) and/or experimental manipulation using corticosterone implants (Goutte et al., 2010) may help to elucidate the patterns we found.

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