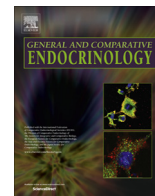




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Physiological and fitness correlates of experimentally altered hatching asynchrony magnitude in chicks of a wild seabird



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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; Merklings 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 (Merklings 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 (Merklings 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 (Merklings et al., 2013). Males, which grow faster and reach a larger size than females near fledging (Merklings 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 Merklings 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 \pm 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

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