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Effect of experimentally increased adult foraging effort on the offspring in black legged kittiwakes (*Rissa tridactyla*)

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Cover photo: Kittiwake, Kongsfjorden, Svalbard. Photo by Rune Smalås

PREFACE

This Master`s thesis has been written at the department of Biology, NTNU, Trondheim. Fieldwork was done in July-August 2010 in Kongsfjorden, Svalbard, financed by the Norwegian Polar Institute (NPI). The Lab analysis has been done at NTNU (sexing) and Centre d'Etudes Biologiques de Chizé (CEBC), France (CORT). Under the watchful and patient supervision of Prof. Claus Bech (NTNU) and doctoral research fellow Elin Noreen (NTNU). It's been hectic at times, but I have always known that you would be there to bring support and feedback whenever I've needed it. I have learned immensely during this time, and I know I'm going to look back at this time with great joy.

These last couple of years have been full off new experiences, and wonderful moments. I want to give a big thanks to all those who have joined me in the field, and made Ny-Ålesund into one of the best experiences in my life. Thanks to Elin, for her fantastic guidance and determination, those were some pretty heavy ladders. Thanks to Claus for being such a calm an assertive figure. Here's to you and Ida for fixing me, that day when I broke.

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Rune Smalås

SAMMENDRAG

Krykkja (*Rissa tridactyla*) er en av de mest grundigst studert sjømåkene vi har, og mye av deres hekkeadferd og fysiologi i forbindelse med hekkeperioden er i stor grad dekket av tidligere studier. Dens habitatvalg gjør den i stand til å dekke det meste av kystlandskapet på den nordlige halvkule, fra Spania i sør til Svalbard i nord. Og av nettopp denne grunn opplever denne arten en høy grad av variasjon når det gjelder miljø under hekkesesongen., noe som igjen fører til store svingninger i hekkesuksessen fra år til år. I et bevaringsøyemed er det spesielt viktig å kunne gi gode estimater for miljøfaktorerers innvirkning på hekkesuksessen, og fuglebestanden som en helhet. Ett skritt på veien mot slik kunnskap er å måle responsen hos ungene, med tanke på vekst og stress, når deres foreldre utsette en kjent økning i energiforbruk. Denne fremgangsmåten er grunnlaget for denne studien.

Langtlevede arter som krykkja, har lenge vært antatt å maksimere sin fitness ved at foreldrene begrenser investeringen til et fast nivå ved hvert hekke forsøk. Ved å manipulere vingestørrelsen hos foreldrene ved starten av klekkeperioden, skapers det et handicap kjent handicap hos eksperimentgruppa. Ved å måle effekten denne behandlingen har på den generelle kroppskondisjonen (BCI) hos foreldre og unger, samt måle forskjeller i grunnnivået av Corticosterone (CORT) hos ungene, ønsker denne studien å undersøke virkningen av de økte energikostnadene forbundet med vingeklippeingsprosedyren. Vingearialet til foreldrene ble redusert, noe som medførte økte flyvekostnadene i forbindelse med matsanking. Effekten denne prosedyren har, sammenlignet med kontrollgruppen, og med tanke på kjønn, er forsøkt belyst i denne studien.

Avkom til vingeklippte foreldre viste ingen signifikant reduksjon, verken på BCI eller CORT nivået sammenlignet med kontroll reir. Hva gjelder CORT nivåene, viste dataene en positiv trend for eksperimentfuglene. Hvor kyllinger tilhørende eksperiment reir viste betydelig lavere CORT nivåer for større unger enn de observert i kontroll reir. Både hanner og hunner så ut til å få den samme behandlingen av sine foreldre, ettersom det ikke ble funnet noen signifikant forskjell i størrelse, BCI eller CORT nivåer mellom kjønnene. Effekten på foreldrene viste heller ingen signifikant forskjell mellom behandlingsgruppene hva gjelder foreldrenes BCI eller vekttap. Men mellom fedre og mødre ble det observert en signifikant forskjell med tanke på prosentvis vekttap, hvor mødre ble funnet å tape en større prosentandel av sine kroppsmasse igjennom hekkeperioden. Dette kan tolkes som en større vilje til å investere i nåværende hekkesesong hos mor, enn den som observeres hos far.

Det ble også observert en signifikant forskjell med mellom vingeklippede par, og kontrollparene, med tanke på rollebytte i forbindelse med matsanking og reirvakt, hvor det vingeklippte foreldre hadde en betydelig lavere frekvens på vaktbytte, sammenlignet med kontrollgruppen. Til tross for resultatene funnet med tanke på reirvaktene, kunne det som nevnt over ikke detekteres noen betydelig negativ effekt fra vingenklippen, verken på avkomme eller foreldre. Denne studien kan derfor ikke si noe definitive med tanke på teoriene knyttet til foreldreinsats under hekking hos krykkja. Å fastslå om det var selve enten det var fra selve inngrepet, miljøfaktorer eller andre, til nå ukjent effektorer som var grunnlaget for dette noe svake resultatet vites ikke. Men blant annet til at ingripen knyttet til den eksperimentelle prosedyren, i dette nok var for liten til å gi et kraftig nok handikap, og dermed gi signifikante data.

Selv om denne studien til en viss grad mislyktes i sitt forsøk på gi ett bedre bilde av trade-offen mellom foreldre og avkom, samt kjønnsrelasjoner vedrørende dette. Ble det imidlertid funnet en veldig sterk korrelasjon ($p = 0,006$) mellom tiden benyttet ved taging av blodprøvene til CORT analysene, og de resulterende CORT nivåene- Ett resultat som galdt, også i tidsintervall på under 3 minutter. Disse resultatene kan tyde på at den allment aksepterte grensen for å kunne måle ett relativt upåvirket grunnnivå for CORT hos sjøfugl, med 3 minutter øvre prøvetakingstid, trolig kan ha sine begrensninger når dette skal måles hos kyllingene.

ABSTRACT

The Black legged Kittiwake (*Rissa tridactyla*) is one of the more extensively studied seagull species, and much of their nesting behaviour and physiology concerning the breeding period has already been examined to a high degree. Its habitat choice is such that it has been able to cover much of the costal habitats on the northern hemisphere, from Spain in the south to Svalbard in the north. For this reason it encounters a high degree of variability when it comes to environmental challenges during its breeding season, leading to large fluctuations in inter-annual breeding success. As the environmental factor play such an important role in conservation, the ability to accurately estimate its effects on sea-bird populations, is of outmost importance. One step towards acquiring such knowledge is to measure the effects on the nestling, when exposing their parents to a known increase in energy expenditure; a procedure attempted in this study.

Long-lived species, like the Kittiwake, have long been thought to maximise their fitness by restricting parental investment to a fixed level in each breeding attempt. By manipulating parental flight wing size at the start of the hatching period, we induced a handicap on the experimental nests. By measuring body condition (BCI) of parents and chicks, in addition to the baseline corticosterone (CORT) levels of the nestlings, this study aimed to investigate whether or not the offspring in the experimental nests would suffer any detrimental effects from increased foraging costs to their parents, by wing-clipping, in comparison to offspring of unmanipulated parents; and whether or not offspring gender played any role in this context.

The offspring of wing-clipped parents showed no significant detrimental effects, neither on body condition or CORT levels in relation to the control nests. With regard to the CORT levels, the data actually suggested a more positive outcome, significantly lower CORT levels for larger nestlings, in the experimental nests than what was found for the control nests. Both males and females seemed to experience the same investment, as there was found no significant difference in size, BCI or CORT levels between them. The effect on the parents also did not show any significant difference between the groups on BCI or weight loss. Neither father nor mother showed any appreciable difference in their investment, measured as their BCI or on weight loss, although mothers was found to loos a larger proportion of their body mass, suggesting that they are willing to assist in a larger extent during chick rearing, in

comparison to fathers. There was also detected a difference in nest attendance, where the treatment actually appeared to give a significant difference, with wing-clipped couples spending a longer time between each nest attention swap. Despite the results on the nest attendance, the lack of a considerable detrimental effect from the wing-clipping procedure could not be detected neither on parents nor the offspring. This study was therefore unable to say anything definitive with regard to parental investment theories. It would seem that the experimental procedure in this case was too weak to give a significant handicap, whether this was from the procedure itself, environmental factors or other, so far, unknown effectors.

Although this study failed in its investigation on parent nestling tradeoffs, and gender relations regarding this; It has however, found a very strong correlation ($P = 0.006$) between handling time during blood sampling and CORT levels in time intervals below the 3 minutes. This suggests that the widely accepted limit of 3 minutes handling time when sampling baseline CORT levels might not be valid with regard to chicks during their growth phase.

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1 INTRODUCTION

1.1 PARENTAL TRADEOFFS

To raise offspring is one of the most energetically expensive periods in the life of an adult animal. This is especially true for birds nesting in arctic waters (Markones et al. 2010; Moe et al. 2002; Tulp et al. 2009). Avian parents will, during a breeding attempt, face a trade-off between their investment in the current breeding attempt and future opportunities for reproduction (Barbault 1988; Erikstad et al. 2009). Investing too heavily in their current offspring could, in these kinds of situations, reduce the parental body condition, energy stores and survival; leading to a reduction on the total lifetime fitness for the parents (Golet and Irons 1999; Golet et al. 1998; Langseth et al. 2000; Martin 1987; Nordstad 2009). As even a small reduction in the survival of the adult in a long-lived species can lead to a large reduction in its lifetime reproductive success, it has been proposed that utilizing a fixed amount of energy in each breeding attempt could be a way to maximise the individuals lifetime reproductive success (Gonzalez-Solis and Navarro 2007). However, for long-lived seabirds living in a highly stochastic environment, it has been argued that a high rate of flexibility in parental investment would be favoured in order to take advantage of the good years and decrease the losses in bad ones (Harding et al. 2009a). Even though flexibility in parental effort has been shown in populations of black legged kittiwakes (*Rissa tridactyla*) (Golet et al. 1998), the validity of this conclusion has been questioned with regard to populations living close to the northern borders of the species distributional range (Welcker et al. 2010). Likewise, the period from hatchling to fledgling, particularly the early nestling stage, represents a highly energetically demanding life stage for the young in many birds (Bech et al. 1988; Gebhardt-Henrich and Richner 1998; Klaassen et al. 1989), where the energetic costs to a large extent is determined by hatching pattern, growth rate and brood size (Martin 1987). During this stage of their life, the nestlings are extremely dependent on their parents and their investments in raising their young (Coulson and Porter 1985; Huin et al. 2000).

1.2 SEXUAL SIZE DIMORPHISM

The amount of parental investment can, in addition to the factors mentioned above, can be further influenced by the sex of the offspring (Brotherton et al. 2001; Cluttonbrock et al. 1985). If a parent gets higher total fitness from raising one sex rather than the other, this may

bias the allocation of resources to that sex, resulting in either a larger numerical production of that sex (Trivers and Willard 1973; Weimerskirch et al. 2005), or providing one sex with larger quantity or better quality of food (Brotherton et al. 2001; Harding et al. 2009a; Hewison and Gaillard 1999; Magrath et al. 2004).

Many avian species show a significant sexual size-dimorphism (SSD), where the offspring of the larger sex generally exhibits a greater food requirement compared to the smaller sex. The consequences of food shortage might therefore have a more dramatic effect on the larger sex, and might to some degree explain the higher mortality observed in the largest sex of both male and female biased sex-dimorphic species (Anderson et al. 1993; Polo et al. 2006; Torres and Drummond 1997). However, even in species where there is little or no SSD, it is reported that the successful rearing of a male can be more costly than rearing a female (Addison et al. 2008; Fargallo et al. 2002; Fletcher and Hamer 2004; Grossman 1985; Harding et al. 2009a). As the effects of starvation or deprivation of food might be more severe for males, this might make the parents bias their allocation of food toward their male offspring even when there is little or no SSD (Råberg et al. 2005; Stamps 1990).

1.3 STRESS RESPONSES

In an ever changing environment, animals are expected to adopt their behaviour in response to a stochastic environment. These kinds of modifications on their behaviour are expected to promote survival and thereby increase their fitness. A large range of behavioural responses can be employed in response to such events, and may include modifications of behaviours associated to foraging activity, nest attendance, feeding of young in adults, and changed behaviours of begging and activity in the young (Schwabl and Lipar 2002). These kinds of behavioural and physiological responses to environmental stress are called the stress response. It is thought to mainly be mediated by hormones originating from the hypothalamo-pituitary-adrenal (HPA) axis (Nelson 2005) and includes among others; cytokines, catecholamines and glucocorticosteroides (GCs) (Nelson 2005).

In response to endogenous or environmental cues, originating from external stressors, higher brain centres will induce the hypothalamus to stimulate the release of corticotrophin releasing hormone (CRH). CRH, in turn, stimulates the anterior pituitary to release adrenocorticotrophic hormone (ACTH), which acts upon the adrenal cortex to synthesise GCs (Harvey et al. 1984; Schwabl and Lipar 2002). GCs, along with other hormones mentioned above, are thought to be the main mediators allowing for rapid readjustment and support of behaviour and

physiology, and would thereby act to retain the homeostasis when facing an unpredictable and changing environment (Brown et al. 2005; Carsia and Harvey 2000; Goutte et al. 2010a; Holmes et al. 1992; Lanctot et al. 2003; McEwen and Wingfield 2010; Romero and Wikelski 2001; Sapolsky et al. 2000).

1.3.1 CORTICOSTERONE

One of the main GCs regulating the homeostasis in birds is thought to be Corticosterone (CORT). Its role in regulating the homeostasis is related both to acute and long term stressor responses (Brown et al. 2005; Goutte et al. 2010b; Romero and Wikelski 2001), made possible from the actions of two different types of receptors, with their different affinities to the CORT hormone (Holmes et al. 1992). One therefore has to differentiate between the baseline CORT level, expressing its long term response to the environment, and the acute stress induced CORT level, resulting from immediate threats to the individual's survival (McEwen and Wingfield 2010). Heightened CORT levels due to such acute stressors have been shown to direct the behaviour of the animal away for non-essential activities, triggering an emergency life-history state (Wingfield et al. 1998).

In adult birds, the baseline CORT level affects behaviours such as regulation of foraging activity, and mobilisation of stored energy reserves (Larsen 2009; Shultz et al. 2004). In addition, chronically elevated levels of CORT may induce a large range of detrimental effects, such as decreased immune function (Broggi et al. 2010), and can affect both territorial and parental behaviours; including abandonment of their young (Angelier et al. 2007; Kitaysky et al. 1999a; Silverin and Sharp 1996).

In precocial species, such as domestic fowl, the ontogeny of the adrenal steroidogenic function has been well studied (McNabb 2007). It has been shown that the HPA axis is functional even during the embryonic development. In these species you will typically find an increase in GC midway through the incubation period, and a peak at the hatching stage, followed by a gradual decline in plasma CORT levels down to adult levels. Mild stress, due to restraint in these early stages of the ontogeny, can in some instances lead to a chronically increased CORT levels (Holmes et al. 1992) a factor suspected to reduce the survivability among the young (Goutte et al. 2010b; Shultz et al. 2004).

Kittiwakes, being semi-precocial, are believed to have a well functioning HPA-axis even during the early nestling stages (Kitaysky et al. 1999b). Kittiwake nestlings have even been shown to have CORT plasma levels close to those of adult birds (Kitaysky et al. 1999a). Food

shortage in nestling kittiwakes has been shown to reduce the nestlings fat reserves (Jodice et al. 2008), and thereby triggering mechanisms which ultimately results in an increase in the circulating corticosterone level (Kitaysky et al. 1999a), resulting in a more intensified begging by the chick (Kitaysky et al. 2001). Because begging is one of the few ways in which chicks can express their physical well-being, their parents will often respond to increased begging by feeding the chick more rigorously (Hamer et al. 1999).

1.4 SIBLING COMPETITION

In addition to the problems described above, siblings will most often have to compete for limited parental resources, giving rise to sibling competition. A larger chick will have a clear competitive advantage over its smaller sibling, and thereby deprive some of its sibling's share (Polo et al. 2006). This can result in severe detrimental effects on growth, development and future life expectancy (White et al. 2010; Young et al. 2010). However, this kind of competition do not always seem to affect the smaller siblings too severely (Groothuis et al. 2007).

1.5 THE EFFECT OF MANIPULATING FORAGING COSTS

Harding et al. (2009b) studied the little auks (*Alle alle*) at Kap Höegh, Greenland. They explored the impact of an experimentally increased foraging cost, in the form of wing clipping on one (single) parent would have. Including the effects this would have on the family of this sexual monomorphic seabird, and whether these effects depended on sex of the offspring. Their results showed that the chicks from experimental nests fledged in a poorer condition, with a lower body mass and higher CORT levels. Male chicks were able to maintain a higher growth rate and fledgling weight compared to the females. Additionally, the results in addition showed that clipped parental birds lost a similar proportion of their initial mass regardless of the sex of the chick. The partner of the clipped parental birds, however, lost more body mass when rearing a son. The study showed that adult little auks are flexible with regard to their parental effort. This pertain both to the behaviour of their partner, and the sex of their offspring. The study suggests that the partner of the wing-clipped bird is able to compensate for the handicap inflicted upon its mate. In addition, it indicates that sons are more costly to raise, in comparison to daughters.

1.6 AIM OF THE STUDY

The present study aims at addressing this, by obtaining data on growth, fledgling weight and hormonal levels in chicks of adult, wing-clipped, and control kittiwakes. If the fixed investment strategy, which has been suggested for kittiwakes breeding in Svalbard (Welcker

et al. 2010) holds true, parent kittiwakes will not, unlike little auks, try to compensate if the costs associated with chick raising increases.

The present study aims to investigate how an experimentally increased foraging cost in adult breeding kittiwakes, in the form of wing-clipping, will affect the chicks, and if there will be a more severe effect on one sex compared to the other.

If the wing-clipped adults follow a flexible investment strategy, we expect that both parents take to sacrifice energy reserves, to be able to compensate for the increased energy demands connected with transportation to and from the foraging areas. The chicks in the experimental nests will therefore not suffer any ill effects, and consequently the experimental chicks are expected not to show any reduction in growth rate or fledgling mass compared to chicks in control nests. In addition their CORT levels are expected to be the same as those observed in the control group.

In contrast, if the wing-clipped adults follow a fixed investment strategy, the parents will not compensate for the increased energy demands with regard to their young. This is expected to result in a reduction of the overall resources allocated to the nestlings in experimental nests, compared to control nests. The experimental chicks would hence suffer ill effects, reflected in a lower growth rate, lower fledgling weight, lower body condition (BCI) and a higher CORT level compared to control nests (Table 1).

Table 1. Predicted outcomes from manipulating parental foraging costs. Showing the expected effects on growth rate, fledgling mass, body condition (BCI) and CORT levels. As predicted by either the flexible- or fixed investment hypothesis.

<i>Parameters</i>	Hypothesis	
	Flexible investment	Fixed investment
Growth rate	not affected	reduced
Fledgling mass	not affected	reduced
BCI	not affected	reduced
CORT level	not affected	Increases

2 MATERIALS AND METHODS

2.1 STUDY AREA AND MODEL SPECIES

The study was conducted from July to August 2010 on the island of Blomstrand in Kongsfjorden Svalbard (78° 59' N, 12° 07' E). Kittiwake chicks from three sub-colonies on the island were used.

The black legged kittiwake is a long-lived, medium sized, circumpolar seabird, and is common on the coast of Norway and Svalbard. It feeds mainly on small pelagic fish; they breed in large cliff colonies and can live up to 19 years of age. They lay 1-3 eggs in each breeding attempt, with an ordinary nest containing 2 eggs, with a hatching interval of 1-2 days between the eggs (Strøm 2006). Both adult and chick kittiwakes show sexual size dimorphism with males having a larger body mass (10.2%), head length (4.5%), wing (2.8%) and tarsus (3.5%) compared to females (Helfenstein et al. 2004; Noreen 2007). The kittiwake is a socially monogamous species, where parents share the work of nest attendance and foraging trips.

Kittiwake chicks are highly dependent on their parents. Lacking homeothermy at hatching, they are totally dependent on their parent for both sustenance and body temperature the first 6-8 days in their nestling period (Barrett 1979), and are normally brooded until 15 days of age (Moe et al. 2002; Noreen 2007). Fledging occurs 5-6 weeks after hatching, but the chicks are still dependent on parental care, and stay in proximity to the nest, being fed by their parents, until migration occurs (Cam et al. 2003; Strøm 2006).

2.2 FIELD PROCEDURE

From the main colony on Blomstrand, 25 control and 25 experimental nests were randomly selected among the breeding population in three sub-colonies. In the experimental group, both parents were handicapped by reducing their wingspan as describe below. All birds were ringed, weighed, measured and manipulated before chick hatching occurred. During the incubation period, nest checks were conducted every other day from 3rd – 9th of July, after which the main hatching period had ended. Nest Checks was also conducted on 13th, 17th, 21st, 29th of July and 6th of August. Biometric data and blood samples of the adults were taken during the wing manipulation, and later during manipulation for another study 15 Days later, estimating the increased adult energy expenditure resulting from the wing clipping procedure

(Welcker et. al. Unpublished data). The biometric data and blood samples were taken at the same time as described in section 2.5.

2.3 MANIPULATION OF THE ADULT FLYING COSTS

Using the procedure described in Gonzalez-Solis and Navarro (2007) we reduced the length of the first three primaries, shortening the first primary (P1) by 3 cm, while the rest was adjusted to give a smooth transition in the shape of the wing. This has been shown to result in an approximately 5-10% increase in flying costs (Harding et al. 2009a). The manipulation was done at first sign of hatching, and with no more than two days between partner manipulations. First manipulation occurred 2nd of July, and the last one occurring 3rd of August

2.4 NEST ATTENDING AND FORAGING TRIPS

During the chick raising period, we studied the frequency of parental shifts in nest attendance by noting the gender of the parent attending the nests in 20 minutes intervals for a continuous 8 hour period on three separate dates (18th of July, 19th of July and 23rd of July), early in the chick raising period. All three sub colonies were sampled at the same time every 20 minute. The data was collected by taking observational notes of the head colour of the attending bird (Blue = male, Red = female, No colour = Squatter). The observations were done during the mid day to late evening period on the different dates (13:30-21:30 on 18th of July; 11:00-19:00 on 19th of July and 10:50-19:00 on 23rd of July). A bird was noted as attending only when they were present on the nest itself. Proximity to the nest was not taken into account.

2.5 CHICK CONDITION

Both biometric measurements and blood samples used in sexing and CORT level estimations were taken 26 days after hatching of the alpha chick. All chicks in the nest were handled at the same time.

2.5.1 BIOMETRICAL MEASUREMENTS

Biometric measurements of the chicks were obtained 26 days after hatching. A spring balance (type Federwage, accuracy to 1.0 g) was used to measure the body mass by placing the chick in a bag, weighing it, and subtracting the weight of the bag. Both skull length and tarsus length were measured with a sliding calliper (accuracy to ± 0.1 mm). The Skull length (head plus bill) was measured parallel to the cutting edge of the bill, from the caudal tip of the bill to the posterior tip of the skull. The length of the tarsus bone was measured by bending the distal toes 90° relative to the tarsus, thereby creating an edge in the joint that functioned as a fixed point for the calliper, measuring from that distal edge to the more medial place notch on the

back of the inter-tarsal joint. Wing length was measured with a stopped ruler from the carpal joint to the tip of the longest primary.

2.5.2 BLOOD SAMPLING

Blood samples were taken, using a syringe, to estimate sex and corticosteron levels, in addition to telomere length, data taken for another study (Bech et. al., unpublished data). A total volume of approximately 0.8 ml (< 1mL) blood was taken, 0.4 mL plasma, for CORT levels; 0.4 mL plasma, for Telomere length and a small droplet, <10 μ L plasma, used for sexing. The samples used for molecular sexing was stored on 96% ethanol. The blood samples for the CORT analysis were extracted in the field, all within 3 minutes after removing the chicks from their nest. Separation of plasma was done in the field and immediately (within 5 minutes after extraction of a sample) frozen in a liquid nitrogen canister for further storage in the field. Long term storage was done in a -80°C freezer.

2.6 ANALYSIS

2.6.1 CORTICOSTERON LEVEL

The CORT level analysis was conducted at Centre d'Etudes Biologiques de Chizé (CEBC) in France.

The radioimmunoassay (RIA) procedure described by Lormee et al. (2003), following the procedure for steroid hormone extraction described by Mauget et al. (1994) was used to estimate the CORT levels. The RIA uses radioactive labelling of antigens specific for the antigenic substrate of interest, in this case corticosterone. The inhibitory effect, caused by the antigen in question (the sampled antigen of an unknown concentration), upon the labelled antigens binding rate to a substrate specific antibody, is used to find the unknown concentration. This is done by doing a comparison between simultaneous preparations of standard and unknown mixtures, each containing the same amount of labelled antigen and antibody. Based on the ratio found between antibody-bound and free labelled isotopes in these mixtures a standard curve for binding affinity is constructed, from which the unknown concentrations of antigen can be estimated (Berson and Yalow 1968).

2.6.2 MOLECULAR SEXING

Due to minute differences in chick size, and no practical difference in plumage, sexing was done using a molecular sexing technique based on the sex chromosome. In birds females are the heterogametic (ZW) sex, carrying both the CDH-1-Z (Chromo-helicase-DNA-binding) gene and the CHD-1-W gene (Griffiths et al. 1998). While males are homogametic (ZZ),

carrying only the small CDH-1-Z gene. With the use of polymerase chain reaction (PCR) the amount of CHD gene was greatly amplified. Gel electrophoresis allows for the separation of the two gene variants where the smaller CHD-1-Z gene will move more readily through the gel matrix. Exploiting the fact that males are homogametic (ZZ), and females have the heterogametic variant (ZW), it makes the detection of W and Z chromosomes a reliable way to sex the birds (Fridolfsson and Ellegren 1999).

A modified version of the Chelex extraction method-described by Walsh et al. (1991)-was used to extract the DNA to be used in the PCR reaction. A 5 % Chelex 100 resin (Biorad, Hercules, CA, USA) solution could isolate and extract the avian DNA from a small blood sample (<1µl). In this procedure a total reaction volume of 10 µl was used for the PCR. The mixture consisted of 0.05 µl Taq DNA polymerase, 1.0 µl 10xPCR buffer, 2.0 µl Q-solution from the Taq PCR Core Kit (Qiagen, West Sussex, UK), 0.4 dNTPs (10 mM, ABgene, Surrey, UK), 0.6 µl MgCl₂, 1.0 µl of each primer (10 µM, P2 and P8) and 2.0 µl DNA-template (40-120 ng genomic DNA). The PCR process starts by a 94°C DNA denaturation step for 3 min. With 35 succeeding cycles of: 94°C for 30 sec., annealing at 46°C for 45 sec and elongation at 70°C for 45 sec. The ending procedure consisted of a elongation step at 70°C for 10 min. Gel electrophoresis in a 2% agarose gel containing ethidium bromide, using a standard TBE buffer for 1 hour, completed the separation of the two genotypes, visualised under UV-light.

2.7 VARIABLES DEFINITION AND STATISTICAL ANALYSIS

All statistical analysis was performed using PASW 18.0 (SPSS Inc. 2010). Graphs were made in SigmaPlot 12.0 (Systat software Inc. 2011). All tests were two-tailed with the significance level set at $P \leq 0.05$. Means and parameter estimates were obtained using general linear models (GLM), and are given with standard error (\pm SE). Pearson correlation analyses were used to look for possible relationships between continuous variables.

A body condition index (BCI) was calculated separately for male and female nestlings, using body mass as the dependent variable in a GLM. A factorial dimension reduction, also called a principle component analysis (PCA) was used, with tarsus length, skull length and wing length as the three variables, to get one collaborative variable from those three. Both the PCA variable and age, were set as covariates in a GLM with body mass as the dependent variable, separate GLMs were taken for each sex. The resulting standardised residuals resulting from this procedure is the BCI for the chicks, and these residuals were used in the study as an

expression of the general wellbeing of the nestling. Pre hatching data, taken during the wing clipping procedure, were used to calculate the BCI for the parents. Using the collaborator variable from a PCA of tarsus-, head - and wing length, a similar GLM to that of the nestlings was taken, with body mass as the dependent variable. The GLM was taken separate for each sex, and the standardised residuals were used as the BCI of the parents.

GLMs were used to check for sexual size dimorphism in the nestlings. The mid nestling period of sampling, and therefore the short age span available in this study, suggested that a linear model could be appropriately used despite the fact that the overall growth curve of the nestlings should be sigmoid. The effect of age analysed in relation to hatching date and sibling relations, as an indicator on its overall strength as an explanatory variable.

A strong relationship between the baseline CORT levels, and the handling time taken during the blood sampling was detected. A linear regression of handling time vs. baseline CORT level was conducted, and the resulting standardised residuals were later used as an approximation of pre-handling baseline CORT. There was not observed any significant difference between sex or group on this time*CORT relation, so the standardised residual values from the CORT*handling time regression was taken as an expression on the population as a whole.

These corrected CORT values, the residuals from the linear regression described above, was used in GLMs to analyse its relation to BCI of the chicks and parents, and chick age, sex, sibling relation and hatching date between the groups. Between the corrected CORT value, and Chick BCI there was also detected a strong correlation. These; together with Group were analysed in a GLM to check for significance, with BCI as the dependent variable, group as the fixed, and CORT as a covariate. Because of a strong significant trend in this GLM, there was also conducted an analysis using a macro for SPSS named MODPROBE described by Cohen (2003) to define the simple slopes and non simultaneous Johnson-Neyman Significance region (Hunka and Leighton 1997) describing the area with significant differences between the two groups.

2.8 PERMISSIONS

Permission to carry out the work in the kittiwake colony was provided by the Governor of Svalbard (Sysselmannen), while permission to perform the wing clipping experiment was given by the Norwegian National Animal Research Authority (Forsøksdyrutvalget).

3 RESULTS

LEVELS AND DYNAMICS IN BIOMETRIC DATA AND CORT LEVELS

All mean values of the nestling measurements are given in table 1 in the appendix. All parameters used in this study fulfilled the Shapiro-Wilk test of normality, and subsequent tests are done with the assumption of normality. There was not observed any strong tendency for sexual size dimorphism in the kittiwake nestlings in the present study, neither within the control or experimental groups, nor on the population as a whole. The only exception was the tarsus length within the control group, which appeared to be slightly larger in females (males: 34.06 ± 0.31 mm, females: 35.16 ± 0.40 mm, $P = 0.038$). Age showed a clear explanatory effect on body mass, skull length, tarsus length and wing length, both on the population as a whole, and within the control group (see appendix table 2 and 3), with sibling relation, (whether the chick is a alpha, beta or singleton), as a strong covariate. However, none of the effects from the variables within the experimental group were statistically significant.

A strong significant correlation between the measurements of baseline CORT levels and the sampling time was detected ($R^2 = 0.115$, $t = 2.820$, $df = 61$, $P = 0.006$, Figure 1). To correct for this confounding effect the standardised residuals from this linear regression were used to represent the CORT-values in all other statistical test.

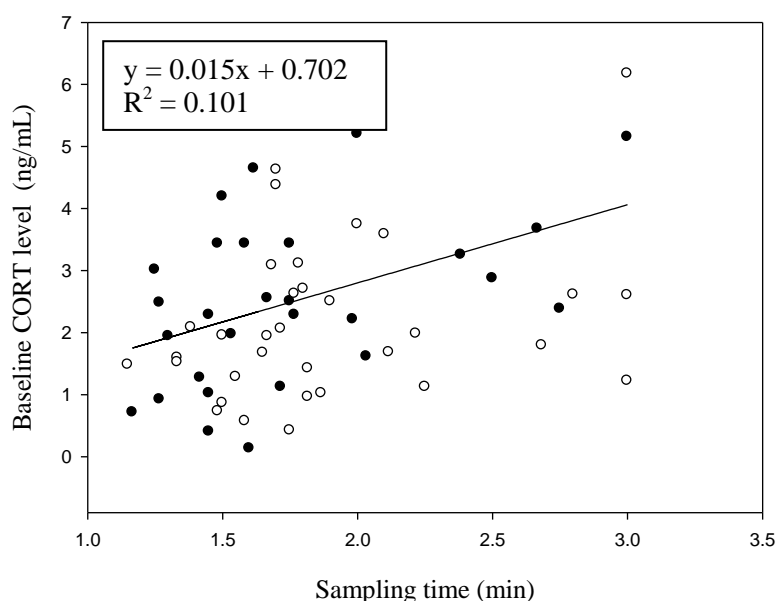


Figure 1: Baseline CORT value as a function of the sampling time. Showing male (○) and female (●) nestling data. The regression line shows the relationship between the CORT level and the time taken during sampling. ($r = 0.340$, $P = 0.006$).

EFFECT OF GROUP TREATMENT

No significant effect of experimental treatment was found on levels of chick CORT, neither between groups (ANOVA: $F_{1,61}=0.044$, $P=0.836$, Figure 2.), nor between gender (ANOVA: $F_{1,61}=0.001$, $P=0.969$). Likewise BCI did not show any significant difference between the groups (ANOVA: $F_{1,61} = 0.902$, $P = 0.346$), or between gender (ANOVA: $F_{1,61} = 0.034$, $P = 0.855$). Experimental chicks did not have significantly higher CORT levels or BCI (Table). Weight loss of adults did not show any significance on losses in measured grams. There was however seen a gender related effect on percentile weight loss (ANOVA; $F_{1,90} = 4.393$, $P = 0.039$), with mothers losing on average 2.77 percent more of their body weight (SE = $\pm 1,314$), table 3.

Table 2: indices of the condition of chicks from clipped and control nests, with values depending on sex. I found no significant relationship between groups ($P > 0.35$), and there was no significant interaction between sex and treatment group in any of the indicators ($P > 0.85$).

		Male			Female			Clipped	Control
		Clipped	Control	All	Clipped	Control	All	All	All
CORT (corrected)	n	12	16	28	18	15	33	30	31
	Mean	0.145	0.209	0.177	-0.221	-0.177	-0.199	-0.038	0.016
	SE	0.299	0.241	0.191	0.244	0.249	0.175	0.187	0.180
BCI (chick)	n	12	16	28	18	15	33	61	61
	Mean	0.160	-0.039	0.060	0.133	-0.160	-0.013	0.146	-0.099
	SE	0.318	0.222	0.191	0.260	0.229	0.175	0.186	0.180

Table 3: shows the mean values of adult weight change, in gram and percentile of body weight, depending on group and gender. There was no significant difference between the groups ($P > 0.72$), and no statistically significant sexual difference in grams lost between the first and last weighing. ($P > 0.44$). However there was detected a gender related effect on percentile of total weight lost ($P < 0.04$, see text)

		Paternal			Maternal			Clipped	Control
		Clipped	Control	All	Clipped	Control	All	All	All
Weight loss (g)	n	23	22	45	23	22	45	46	44
	Mean	49.96	48.50	49.23	51.52	54.14	52.83	50.74	51.32
	SE	6.56	23.21	14.89	5.86	19.82	12.84	6.38	21.52
Weight loss (% of body weight)	n	23	22	45	23	22	45	46	44
	Mean	12.69	12.59	12.64	14.89	15.95	15.42	13.79	14.27
	SE	6.01	22.61	14.31	6.70	21.68	14.19	6.39	21.92

This study could not find any statistically significant relation between the nestling body condition, and parental body condition (Figure 2). A correlation between chick condition and percentage maternal weight loss appeared in a Pearson correlation plot ($r = 0.239$, $P = 0.017$). When this correlation was examined in a GLM, with nestling BCI as the dependent variable, and parental percentile body loss and BCI as covariates, neither a within- ($P_{\text{weight}} > 0.358$, $P_{\text{BCI}} > 0.067$), nor between-group effect was detected at a significant level ($P_{\text{weight}} > 0.546$, $P_{\text{BCI}} > 0.107$). Also, see appendix, table 4.

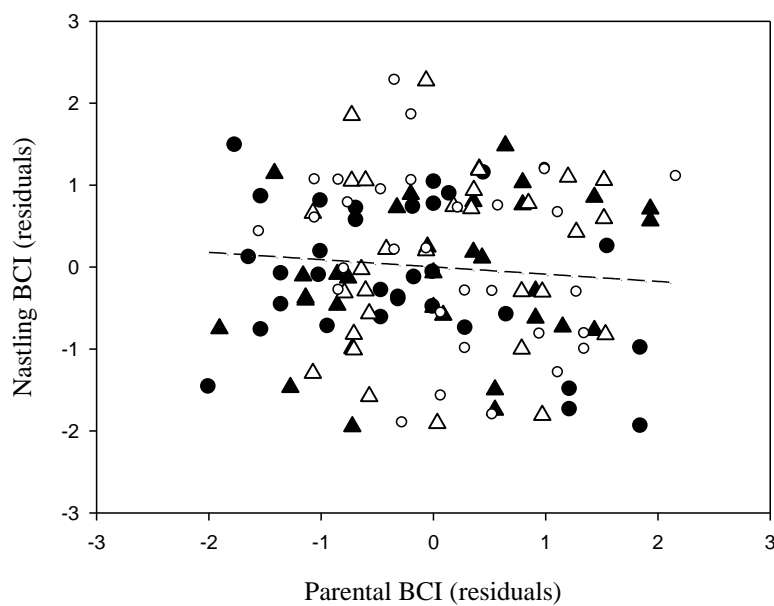


Figure 2: Nestling body condition index (BCI) as a function of paternal (Control: Δ , clip: \blacktriangle) and maternal (control: \circ , Clip: \bullet) BCI. The regression line show the general trend of all data point. It shows no significant trend. None of the sub-groups were found to show any significant correlation either.

3.1 NEST ATTENDANCE

Nest attendance showed a significant difference between the control and experimental group. When using an ANOVA with repeated measures with Greenhouse-Geisser correlation, the mean score for Group*Nest attendance was statistically significantly different ($F_{1,62} = 7.459$, $P = 0.008$). Experimental birds show a significant reduction in number the number of swaps of nest attendance. On average the control birds swapped approximately one more turn compared to experimental birds (Average swaps control birds; 4.50 (SE = ± 0.265); Average swaps wing-clipped birds; 3.36 (SE = ± 0.265)), The two measurements of nest attendance were not significantly different ($P = 0.587$).

3.2 CORTICOSTERON LEVEL IN RELATION TO BODY CONDITION

There was detected a somewhat significant relationship between BCI and the uncorrected values of CORT (ANOVA: $F_{1,60}=4.655$, $P=0.36$), which in a linear regression showing a strong negative correlation of -0.325 ($SE = \pm 0.121$) between the two factors ($R^2 = 0.108$, $t = -2.679$, $df = 59$, $P = 0.01$), with group also showing some explanatory effect (ANOVA; $F_{1,60}=4.348$ $P=0.042$). Although they could not be used as a combined factor, $CORT*Group$ (ANOVA; $F_{1,60}=3.059$, $P=0.086$).

When using the residuals controlling for handling time, CORT gained a lot of explanatory value (ANOVA; $F_{1,60}=7.603$, $P=0.008$), and there was detected a strong statistical significance when group was taken into consideration (ANOVA; $F_{1,60}=5.162$, $P=0.027$), even though group by itself, no longer had any significant explanatory value on BCI (ANOVA; $F_{1,60}=0.902$, $P=0.347$).

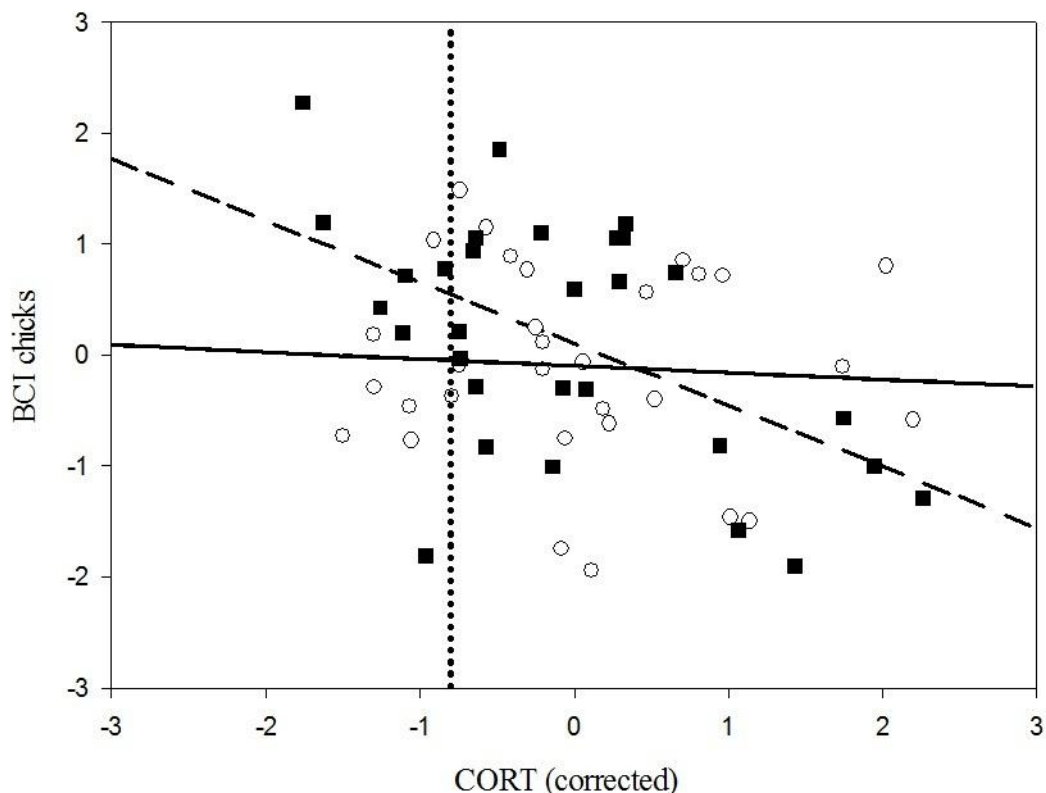


Figure 4: show the trend lines between the BCI residuals for the chicks, and the residual values of the corrected CORT values between control (\circ , solid line) and the experimental chicks (\blacksquare , spaced line). The dotted line show the higher bonds of the Johnson-Neyman significance region., and indicates a significant difference between the two groups in BCI in the area of values below a residual CORT value of -0.8177 , see text.

The negative correlation between CORT and BCI in the nestling, and the possible significance between the groups described above, was further investigated using simple slope procedure, and revealed a very strong model when including both CORT and group ($R^2=0.1819$, $F_{3,57}=4.225$, $P=0,009$). Revealing an increase in R^2 value due to this interaction of 0.062 (from $R^2 = 0.108$, to $R^2 = 0.170$; $F=4.309$, $P=0.042$), and the Johnson-Neyman significance region set to $-0,8177$. i.e. the focal predictor (Group) had a significant explanatory value up until that point (see figure 4).

4 DISCUSSION

SEXUAL SIZE DIMORPHISM

In the present study, I was not able to find any clear trend for sexual size dimorphism in the nestlings of the black legged kittiwake (*Rissa tridactyla*). Although I did see a significant difference in tarsus length within the control group; 1.4% longer tarsus in females as compared to males ($P = 0.038$), but this trend could only be detected within the control group. In previous papers there has been found a clear dimorphism in both nestlings (Noreen 2007) and adults (Helfenstein et al. 2004), with males overall being the larger sex (Nestlings: 9.1% , adults: 10.2%). An even more thorough study on nestling growth rate and size was conducted by Trolid (2008) that SSD did not become significantly different until late in the nestling period, when the chick is close to fledgling age. As the data for this study was taken as early as at 25/26 days of age, it is perhaps not surprising that the biometric data did not show any a statistically significant SSD, other than the difference in tarsus length within the control group. This is not to say that the internal development has not begun to show gender related differences, for instance on the immune system or organ development.

Age showed a significant relationship to body condition, with older chicks (26 days old) being 8.2% larger, on average, compared to the younger group (25 days old). As there was only a one day difference between the age groups, this trend was thought to reflect the sibling relation to a larger degree than actual age, with alpha males and singletons, being in the older group, and beta chicks being in the younger one. This short age span was to be expected, as the data collection for my study was timed to fit with a study concerning, among others, immune competence at mid hatching (age alpha chick 26 days, Noreen. et. al. unpublished data). Therefore, I would expect sibling relation to be the important factor. I was not able to differentiate between the relative importance of these factors, as they are confounded. However, it makes more biological sense for sibling relation to be a “real” effect, than an age difference of only one day. Therefore, sibling relation was thought to be indistinguishable from age, and was used as an explanatory variable in other GLMs.

EFFECT OF SAMPLING TIME

There was detected a very strong correlation between the baseline CORT estimates and the time used when sampling the blood ($r = 0.34$, $P = 0.006$, table 1). Romero and Reed (2005) suggested that a sampling time of under 3 minutes on birds in the field should be a short enough time to avoid the rising CORT levels resulting from the acute stress caused by the

handling. This limit has been recognised as a good guideline when taking CORT blood samples in situ, and has been used in many studies on seabirds (Quillfeldt et al. 2009; Stöwe et al. 2010; Williams et al. 2008), including kittiwakes (Angelier et al. 2007; Goutte et al. 2010a; Goutte et al. 2011; Larsen 2009; Nordstad 2009), and has also been applied on kittiwake nestlings (Brewer et al. 2008a; Brewer et al. 2008b; Harding et al. 2009b; Jodice et al. 2008; Kitaysky et al. 2006; White et al. 2010). My results suggest that nestlings might have a much faster response to acute stressors, compared the time limits Romero and Reed (2005) propose. A rise in CORT levels as a result from acute stressors, such as handling, even before the suggested 3 minutes sampling time. In addition, my data does not show any indication of a lower time limit on this response. A continuous rise in the CORT levels, even from no more than 1 minute of handling time, has been shown. Making it hard to conceive an in situ time interval where the baseline CORT could be independent from the handling time, as the time required to take the blood sample is cumbersome to press below 1 minute. As a consequence of this, nestling baseline CORT levels do seem to be affected by the handling in taking the blood sample. My data suggest a time-dependent rise of the CORT values with a slope of 0.015 ng/mL for each minute. However, the low r value of 0.340 indicates a somewhat low accuracy in the predictions given by this regression line; and this, in addition to an already high inter-annual variation in baseline CORT among kittiwake chicks (Brewer et al. 2008b), suggests that the trend line found in this study is not going to be a good guideline for use in future studies. I have been unable to find other studies indicating a trend as described here, neither as separate studies looking into such a relationship in kittiwake chicks, nor as a part of their analytical methodology when handling data. If, as suggested above, sampling time affects the baseline CORT measurements, even when the handling is kept well below 3 minutes in Kittiwake nestlings, future studies will have to take this into consideration, both during sampling, and as a part of their statistical analysis. It might also imply that older studies on Kittiwake nestlings, dealing with baseline CORT levels, would need to be re-examined to include this parameter. Furthermore, there is no guarantee, and it might seem unreasonable, to assume that this relationship, if it exists, is isolated to kittiwake nestlings alone. If this is the case, then studies on other species involving nestlings would also require re-evaluation, but such speculations go far beyond the scope of this study.

EFFECT OF TREATMENT

In this study I was unable to detect any significant effect of the treatment on those parameters I had used as indicators of the condition of the chick (Table 1, figure 2), suggesting that the wing-clipping treatment had little to no effect on the offspring of handicapped parent. This data would support the flexible parental investment hypothesis of Golet et al. (1998), and stand in stark contrast to the fixed investment strategy postulated by Welcker et al. (2010) for kittiwakes nesting in Kongsfjorden, Svalbard. A recent study conducted by Leclaire et al. (2011) on Kittiwakes living on Middleton island in the gulf of Alaska, also conducted using wing clipping, showing that male kittiwakes exhibited a fixed strategy, with regard to their young; while the females on the other hand showed flexibility in their parental investment.

With regard to the adults, there was not detected any statistically significant effect on body condition. This was not too unexpected, as these were taken early in the manipulation period, and was first and foremost meant as a parameter for evaluating chick condition. With regard to nestling BCI, parental BCI showed a non-significant correlation, both within and between the groups (figure 2). Percentile weight loss of the parents revealed the same non-significant relationship (figure 3) Results that at face value could be taken as an indication for a fixed hypothesis. Although, with the lack of significant effects on their young as well, these results would instead be lending doubts on the assumption that our procedure of reducing the wing length gave a sufficiently strong handicap to provoke a significant response on the physiology of our birds. However, there was found a significant difference between the two groups with regard to nest attendance. The wing-clipped birds showed an average of 3.36, as opposed to 4.50 in among control birds in an 8 hour time period, giving reason to suspect that wing-clipped birds, might need longer periods out to forage for food. In addition, there were detected a significant difference between the parents when it came to weight lost during the breeding period. Mothers lost approximately 2.77 percent more of their body weight ($SE = \pm 1,314$, table 3), compared to that of fathers, possibly reflecting a higher willingness in the females, compared to the males, to invest in current offspring.

It should be noted that in a study by Leclaire et al. (2011), they cut the no 3, 4 and 7 primaries, and the 2 central rectrices, even increasing this to 4 central rectrices in the second year of the study. What impact this was expected to have on the daily energy expenditure is not fully clear from their study. However, it is obvious from the description of their procedure that this was a much more invasive one with regard to the wing manipulation. The procedure

gave significant result, and the results even went as far as to suggest a sex difference in parental investment strategies, similar to the higher maternal weight loss, described above.

We had also noticed during our manipulation procedure that the tip of the wings in many cases could seem rather tattered. Hence, it might be possible that our method of increasing parental energy expenditure might not have made any profound difference on the birds' daily energy expenditure. In addition it must be noted that the summer of 2010 had been a good year for the bird colonies in Kongsfjorden, Ny-Ålesund. There was much bird life in the fjord, and lots of kittiwakes seemed to feed close to the nearby glaciers. So, the travelling distance to the feeding grounds did not necessarily amount to a large cost in the form of energy during this period. The combination of possibly not handicapping the parents enough and a rather good year to raise your young might have caused the impact of the wing-clipping to be masked or reduced.

Despite the above results, a significant correlation was detected between the groups on the regression values of the corrected CORT level and chick BCI (section 3.3). Chicks in the experimental group had a significantly different regression line to that of control birds, on CORT values below -1.8177 on the corrected residual scale. Experimental chicks showed a higher BCI at these lower CORT levels, compared to controls. It almost goes as far as to suggest that the manipulation procedure have been beneficial for the experimental nestling. It also showed that the difference between individuals within the experimental group is much larger, than that of the control group, due to a steeper regression slope. The cause of this is somewhat unknown. If the experimental procedure had an effect, it would be expected an almost identical curve, although in the opposite order, with the control birds exhibiting the kind of slope, experimental chicks show in these results, and vice versa. This result I believe demonstrates the power of corrected for handling time, so that the underlying effects of CORT upon body condition can be better understood. A strong negative correlation between CORT levels and body condition on the population as a whole was detected when calculating for this, and this shows both to the importance of being able to remove noise from the data set, while also confirming the importance of CORT in relation to general well being of kittiwake nestlings.

With regard to the predictions set forward in table 1, There was not detected any statistical significance difference between the experimental and the control group on BCI. So this factor seems to be, not affected, by the experimental procedure. Growth rate and fledgling mass was

not followed actively, because of compromises with other studies, in this study, although one can, by extrapolating the results from the biometric data, postulate that at least growth rate seems to be unaffected, as I was unable to detect any effect from group on, either body mass, tarsus-, head-, or wing length. If the growth rate is unaffected I could also suggest that the effect on fledgling weight would be unaffected. Therefore both growth rate and fledgling weight is asserted as not affected by the experimental treatment. With regard to CORT levels, when correcting for BCI, there was detected a significant difference between the experimental- and control groups, however, this trend was the opposite of the one predicted by the fixed hypothesis described in table 1; that is, within the Johnson-Neyman significance region, chicks from manipulated parents had a lower CORT level relative to BCI, than nestling living in control nests. Over all, this gives some support to the flexible investment hypothesis. This is especially true with regard to a flexible mother, as there was a significant decrease in maternal percentage weight loss, compared to fathers.

CONCLUSION

This study has found very little data to support the fixed investment hypothesis, with regard to kittiwake nestlings living in Kongsfjorden, Svalbard. None of the biometric data showed any significant difference between nestling living with wing-clipped parents, and the control nestlings. The data on CORT levels suggest a reduced baseline CORT levels in correlation with body condition on chicks in the experimental group, as opposed to the control group as, the fixed hypothesis would have it, although the number of swaps on nest attendance between the parents was reduced for the experimental group. It is somewhat unclear whether the trends observed on these parameters are due to a particularly good breeding season, miscalculations concerning the handicap so that it failed to provide a significant effect or other reasons that have thus far evaded my attention. Among the adult birds mothers lost a higher proportion of their total weight as opposed to the fathers, and appear to take on a disproportional part of the chick rearing costs. There was not found any sexual size dimorphism on the offspring, neither within nor between the treatment groups, and parental BCI did not seem to affect their offspring. There was a likely existing sampling time effect on baseline CORT measurements on kittiwake nestlings, even when the blood sampling time is kept well under 3 minutes, suggesting a faster and possibly stronger response to acute stressors in nestling kittiwakes compared to what we find in the adults. I therefore suggests that researchers working on nestling kittiwakes and possibly on other semi-prococial species must be very careful when using baseline CORT as a statistical variable, as handling might provide large deviations from the real baseline levels. I would urge other researchers to confirm or dismiss this hypothesis, as it might have large impacts on the field-, and/or analytical procedures connected to research on chick physiology in Kittiwakes as well as other species.

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APPENDIX

Table 1: Summary of descriptive statistics for body measurements, BCI, Baseline CORT, the time used when taking blood samples and the standardized residuals from the linear regression between baseline CORT and the blood time in kittiwakes chicks from Blomstrand, Svalbard.

Group	Variables	N	Minimum	Maximum	Mean	SE
Combined	Body mass (g)	65	199	475	363.3	6.0
	Skull length (mm)	65	65.80	83.10	76.60	0.4
	Tarsus length (mm)	65	31.60	38.50	34.50	0.2
	Wing length (mm)	65	113	209	184	2.2
	Body Condition Index (BCI)	63	-1.9	2.3	0.0	0.1
	CORT (ng/mL)	63	0.1	6.2	2.3	0.2
	Blood times (mm.ss)	65	01:09	03:00	01:51	00:04
	CORT in relation to time	63	-1.8	2.3	0.0	0.1
	Valid N (list wise)	61				
Control	Body mass (g)	33	214	437	360.5	8.2
	Skull length (mm)	33	67.60	81.70	76.60	0.6
	Tarsus length (mm)	33	32.30	37.00	34.40	0.2
	Wing length (mm)	33	129	209	184.2	3.1
	Body Condition Index (BCI)	32	-1.9	1.5	-0.1	0.2
	CORT (ng/mL)	32	0.4	5.2	2.3	0.2
	Blood times (mm.ss)	33	01:09	03:00	01:44	00:05
	CORT in relation to time	32	-1.5	2.2	0.0	0.2
	Valid N (list wise)	31				
Experimental	Body mass (g)	32	199	475	366.2	8.9
	Skull length (mm)	32	65.80	83.10	76.50	0.6
	Tarsus length (mm)	32	31.60	38.50	34.60	0.2
	Wing length (mm)	32	113.0	205	183.8	3.1
	Body Condition Index (BCI)	31	-1.9	2.3	0.1	0.2
	CORT (ng/mL)	31	0.1	6.2	2.4	0.3
	Blood times (mm.ss)	32	01:10	03:00	01:58	00:06
	CORT in relation to time	31	-1.8	2.3	0.0	0.2
	Valid N (list wise)	30				

Table 2: Summary of a multivariate GLM explaining variation in body mass, skull-, tarsus, wing length and BCI, in relation to sex and age (25-26), between the treatment groups. n=63, female: 33, male: 30. The estimate for sex show females compared to males.

Explanatory	Variables		df	F	Sig.	Estimate	±SE
	Dependent	Index					
Sex	Body mass (g)		1	0.053	0.819	-2.670	10.010
	Skull length (mm)		1	0.916	0.342	-0.742	0.670
	Tarsus length (mm)		1	0.510	0.478	0.197	0.238
	Wing length (mm)		1	0.240	0.626	-1.992	3.512
	Body Condition Index (BCI)		1	0.005	0.942	-0.018	0.003
Age	Body mass (g)		2	5.248	0.008	43.133	13.007
	Skull length (mm)		2	10.312	0.000	3.750	0.870
	Tarsus length (mm)		2	7.269	0.002	1.061	0.310
	Wing length (mm)		2	8.680	0.000	19.410	4.564
	Body Condition Index (BCI)		2	0.399	0.673	0.164	0.282

Table 3: Summary of a multivariate GLM explaining variation in body mass, skull-, tarsus, wing length and BCI, in relation to sex and age (25-26), within the treatment groups. n=63, female: 33 (clipped: 18, control: 15), male: 30 (clipped: 13, control: 17). The estimate for sex show females compared to males.

Group	Variables		df	F	P	Estimate	±SE
	Explanatory	Dependent					
Control	Sex	Body mass (g)	1	2.143	0.155	9.577	12.610
		Skull length (mm)	1	2.392	0.134	1.209	0.781
		Tarsus length (mm)	1	4.796	0.038	0.494	0.314
		Wing length (mm)	1	1.623	0.214	6.732	3.946
		Body Condition Index (BCI)	1	1.226	0.278	-0.125	0.254
	Age	Body mass (g)	2	5.191	0.013	54.857	15.889
		Skull length (mm)	2	13.256	0.000	4.798	1.004
		Tarsus length (mm)	2	7.706	0.002	1.366	0.403
		Wing length (mm)	2	12.030	0.000	26.637	5.073
		Body Condition Index (BCI)	2	1.052	0.364	0.168	0.326
Experimental	Sex	Body mass (g)	1	0.066	0.800	-17.093	16.585
		Skull length (mm)	1	1.367	0.253	-2.754	1.057
		Tarsus length (mm)	1	0.192	0.665	-0.120	0.379
		Wing length (mm)	1	1.658	0.210	-10.968	5.768
		Body Condition Index (BCI)	1	0.132	0.720	0.023	0.367
	Age	Body mass (g)	2	1.143	0.335	28.781	21.704
		Skull length (mm)	2	1.538	0.234	2.453	1.383
		Tarsus length (mm)	2	1.139	0.336	0.684	0.496
		Wing length (mm)	2	0.838	0.444	10.844	7.548
		Body Condition Index (BCI)	2	0.462	0.635	0.147	0.480

Table 4: Summary of GLM parameters of parental body condition and weight loss on nestling body condition. Examining both within and between group effects on

Group	Dependent Variable	Independent variable	Covariate	R ²	t	P	β	SE
Combined	Chick BCI	BCI	Parental	0.042	-0.211	0.834	-0.028	0.134
			Mother	2.552	-10.637	0.107	-0.209	0.128
			Father	0.925	0.985	0.329	0.139	0.141
		% weight loss	Parental	0.363	-0.601	0.546	-0.004	0.007
			Mother	0.081	0.275	0.775	0.021	0.077
			Father	0.025	0.176	0.873	0.014	.0081
Control	Chick BCI	BCI	Parental	1.014	-1.179	0.249	-0.221	0.187
			Mother	2.655	-1.908	0.067	-0.292	0.153
			Father	0.034	0.217	0.830	0.041	0.189
		% weight loss	Parental	0.688	-0.935	0.358	-0.007	0.008
			Mother	0.237	0.549	0.588	0.049	0.089
			Father	0.278	0.594	0.557	0.056	0.094
clipped	Chick BCI	BCI	Parental	0.488	0.642	0.526	0.150	0.233
			Mother	1.931	-1.278	0.212	-0.313	0.245
			Father	0.035	0.172	0.865	0.042	0.246
		% weight loss	Parental	0.007	0.074	0.942	0.001	0.012
			Mother	0.045	-0.193	0.848	-0.027	0.142
			Father	0.143	-0.345	0.733	-0.050	0.146