

# Parent-offspring interactions in a long-lived seabird, the Little Auk (*Alle alle*): begging and provisioning under simulated stress

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Received: 3 May 2016/Revised: 7 July 2016/Accepted: 28 July 2016/Published online: 9 August 2016  
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**Abstract** Long-lived seabirds are good models to study the mechanisms that mediate the parent–offspring interactions. Contrary to studies under natural conditions, experimental manipulations allow us to assess the birds’ reactions in a short time period. We used the stress hormone corticosterone as an independent experimental factor to simulate the stress reaction, to examine changes in the behaviour of Little Auk chicks and parent birds. In the first experiment, we hypothesised that after enhancement of the corticosterone level Little Auk (*Alle alle*) chicks intensify their begging performance and attain a higher pre-fledging body mass than the control chicks. In the second experiment, we hypothesized that parent Little Auks with an increased corticosterone level feed their chicks less frequently and spend less time at the colony than their untreated partners and the control birds. We also expected that chicks with one parent implanted with corticosterone fledge later and with a lower body mass than chicks of two untreated parents. The obtained results supported the above hypotheses. We demonstrated that modification of begging performance in Little Auks constitutes an adaptive mechanism that guards against the decrease in the chicks’ body condition during stressful periods. Even though the provisioning rate in Little Auks can be regulated according to the chick’s needs (expressed by the intensity of the begging

display), it appears that adult birds regulate their provisioning strategy primarily according to their body state. The results suggest that parent Little Auks under stressful conditions will decrease their parental effort and redirect the available energy towards self-maintenance. The study provides novel insights into the behaviour of long-lived alcids using an experimental approach on free-living birds.

**Keywords** Begging · Provisioning · Chick growth · Corticosterone · *Alle alle* · Arctic

## Zusammenfassung

**Eltern-Nachwuchs Interaktionen bei einem langlebigen Seevogel, dem Krabbentaucher (*Alle alle*): Betteln und Versorgen bei simuliertem Stress**

Langlebige Meeresvögel eignen sich gut, um Mechanismen der Eltern-Nachwuchs Interaktion zu untersuchen. Im Gegensatz zu Studien unter natürlichen Bedingungen erlauben experimentelle Manipulationen, die unmittelbare Reaktion der Vögel zu messen. Wir verabreichten das Stresshormon Kortikosteron zur Simulierung einer Stressreaktion und, um Verhaltensänderungen bei Eltern- und Jungtieren zu beobachten. Die Hypothese im ersten Experiment war, dass Küken mit erhöhtem Kortikosteronspiegel ihr Bettelverhalten intensivieren und schwerer werden als die Kontrolltiere. Im zweiten Experiment postulierten wir, dass Eltern mit erhöhtem Kortikosteronspiegel ihren Nachwuchs seltener füttern und weniger Zeit in der Kolonie verbringen als ihre unbehandelten Partner bzw. Kontrolltiere. Wir erwarteten auch, dass Küken von Paaren, in denen ein Elternteil mit einem Kortikosteronpellet implantiert war, später schlüpfen und dabei leichter sind als Küken von unbehandelten Eltern. Die Ergebnisse unserer

Communicated by C. Barbraud.

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Experimente unterstützten unsere Hypothesen. Wir konnten zeigen, dass die Modifikation des Bettelverhaltens beim Krabbentaucher ein adaptiver Mechanismus ist, der einer Verschlechterung der Verfassung während Stressperioden entgegenwirkt. Obwohl die Versorgungsrate beim Krabbentaucher entsprechend dem Bedürfnis der Küken (ausgedrückt durch die Intensität des Bettelverhaltens) reguliert werden kann, scheinen erwachsene Vögel ihre Versorgungsstrategie primär nach ihrer Körperversorgung auszurichten. Die Ergebnisse legen nahe, dass Krabbentaucher in Belastungssituationen ihre elterliche Fürsorge reduzieren und die verfügbare Energie in Richtung Selbsterhalt umlenken. Die Studie liefert neue Einsichten in das Verhalten langlebiger Alken unter Verwendung eines experimentellen Ansatzes bei freilebenden Vögeln.

## Introduction

The allocation of resources between parents and offspring is particularly important for long-lived species. Under limited resources, long-lived parent birds are expected to safeguard their own body condition, rather than to invest in current reproductive output (Ricklefs 1977; Stearns 1992). Thus, a degree of parental investment should be determined primarily by the parents' physiological state and their prospects of survival, whereas chicks may attempt to solicit more food by intensifying their begging performance. In honest signalling, begging displays incorporate information about a chick's energy requirements or chick state, and parents use this as a signal to adjust their provisioning rate accordingly (Cotton et al. 1996). Both begging behaviour and parental provisioning strategies can be determined by fluctuations in the environment, which affect birds during their breeding period. When resources are severely limited, chicks compete with their future siblings.

Seabirds, which are characterised by long life spans, late maturity, and a low annual reproductive output, are good models to study the mechanisms that mediate the parent–offspring conflict. The Little Auk (*Alle alle*) is an Arctic seabird that exhibits one of the highest mass-specific daily energy expenditures and daily weight gain among the Alcidae and other seabird species of similar body mass (Konarzewski et al. 1993; Stempniewicz 2001). A single semi-precocial chick is raised annually, in a nest concealed under the surface, in extensive boulder scree on mountain slopes (Stempniewicz 2001). The chick remains in the nest for 4 weeks (Stempniewicz 1981; Wojczulanis-Jakubas and Jakubas 2012) and both parents contribute equally to chick provisioning (Stempniewicz and Jezierski 1987) until the final week of chick rearing, when some females disappear from the colony 1–3 days before the chicks fledge

(Harding et al. 2004; Wojczulanis-Jakubas and Jakubas 2012). Parent birds might be flexible and adjust their provisioning efforts to variable trophic conditions. Some studies have suggested that Little Auks can compensate for a lower quality of food by increasing the number of feedings (Jakubas et al. 2007; Kwasniewski et al. 2010), whereas others documented a decreased provisioning rate under deteriorated foraging conditions (Welcker et al. 2009; Kidawa et al. 2015). The inconsistency of these results is difficult to explain in natural conditions. Studies on other seabirds, such as the Common Guillemot *Uria aalga* or Atlantic Puffin *Fratercula arctica*, also demonstrated that adult birds invested more energy to buffer nestlings from the consequences of reduced prey availability (Burger and Piatt 1990; Eilertsen et al. 2008).

Contrary to environmental changes, which are slow and difficult to forecast, experimental conditions allow us to predict the birds' response in a short time period. Variable demands of the life cycle, as well as unpredictable and life-threatening perturbations in the environment activate the hypothalamic–pituitary–adrenal axis (Möstl and Palme 2002; Romero 2002; Landys et al. 2006). This results in enhancing the secretion of glucocorticoids, which are the front-line hormones that participate in an organism's response to stress (Möstl and Palme 2002). A high level of corticosterone, which is the main stress hormone in birds, has been suggested to be a reliable indicator of poor condition or health, thus, reflecting how an individual copes with the environment (Bonier et al. 2009). In Little Auks, a higher corticosterone level might also be associated with food deprivation or unfavourable weather conditions (Kidawa et al. 2014). Therefore, corticosterone could be used as an established hormonal indicator of an organism's response to stress, but also as an independent experimental factor that simulates the stress reaction (Kitaysky et al. 2001; Romero et al. 2005; Müller et al. 2009a; Shini et al. 2009; Spée et al. 2011). Experimental manipulations appear to be the best way to predict birds' reactions during unfavourable environmental conditions. The recognised positive corticosterone response to adverse trophic and environmental conditions (Harding et al. 2011; Kidawa et al. 2014) allowed us to artificially enhance the corticosterone level in Little Auk chicks and adult birds, to study changes in their behaviour.

In the first experiment, we studied changes in the begging performance and growth of Little Auk chicks following an experimental increase in the circulating corticosterone levels. We hypothesised that Little Auk chicks intensify their begging in response to increased corticosterone levels and attain a higher pre-fledging body mass than the control chicks. Single-chick broods of Little Auk provide an opportunity to study the role of begging signals in a parent–offspring conflict, without the effect of

sibling competition. Moreover, the role of hormones as regulators of offspring begging performance varies among different bird species (Smiseth et al. 2011), and the begging behaviour of Little Auk chicks has not been studied to date. Changes in begging performance in relation to increased corticosterone levels have been studied mostly in birds with more than one offspring (Kitaysky et al. 2001; Val-larino et al. 2006; Loiseau et al. 2008). Some studies of species with single-chick broods reported contrasting results, with no relationship between corticosterone secretion and begging behaviour in the Tufted Puffin *Fracetula cirrhata* (Williams et al. 2008) or a positive correlation in the Thin-billed Prion *Pachyptila belcheri* (Quillfeldt et al. 2006).

In the second experiment, we investigated changes in the chick provisioning rate and the time spent at the colony by Little Auk parent birds with experimentally increased levels of circulating corticosterone, as well as the growth of their chicks. We hypothesised that adult birds with an increased corticosterone level feed their chicks less frequently and spend less time at the colony than their untreated partners and the control birds. We also expected that chicks with one parent implanted with corticosterone fledge later and with a lower body mass than chicks of two untreated parents. Due to the evident linkage between body condition and survival (Harding et al. 2011), adult birds should govern the degree of parental investment against the negative consequences on their own body condition. Exploring the mechanisms that regulate the parental investment might help to evaluate the trade-offs involved in the reproductive performance in Little Auks, which are particularly important in predicting their response to the worsening foraging conditions in the Arctic (Karnovsky et al. 2010; Kwasniewski et al. 2012).

## Methods

We carried out the study in the Little Auk breeding colony on the Arikammen slopes in Hornsund (SW Spitsbergen; 77°00'N, 15°33'E), which constitutes one of the main breeding areas of Little Auks in Svalbard (Isaksen 1995). We conducted field experiments during two breeding seasons: in July to August in 2012 we carried out experimental manipulations with chicks, and in July to August in 2013 we carried out experimental manipulations with parent birds. Nests were located on mild talus slopes, with breeding densities of ca 1.6 birds/m<sup>2</sup>. In both study years during the period of hatching, we were examining 50 Little Auk nests every 2 days to determine the precise ( $\pm 1$  day) day of hatching of each chick. We ceased regular nest inspections after hatching, to prevent disturbance to provisioning parents until the second week of the chicks' life.

We chose nests with chicks of similar hatching date ( $\pm 1$  day) for the studies.

## Experiment with chicks

In the first experiment, we implanted 15 Little Auk chicks of the same age (10–12th day of life) with self-degradable, corticosterone-releasing pellets (Innovative Research of America, Sarasota, FL, USA; 7.5 mg corticosterone, 7-day release). Additionally, we implanted three chicks with a placebo pellet. We placed the pellets under the skin on the neck through a small incision (ca 0.3 cm), which we closed with tissue adhesive (Surgibond, SMI AG Germany). The experimental treatment did not affect the survival of chicks. Previous studies have shown that exogenous corticosterone administration effectively increases the corticosterone level in birds (Kitaysky et al. 2001; Romero et al. 2005; Bourgeon and Raclot 2006; Angelier et al. 2009; Müller et al. 2009a, b; Spée et al. 2011). For example, Spée et al. (2011) observed a 3.3-fold increase in circulating corticosterone levels within 3 days of pellet implantation. We chose chicks with a similar body mass for the study, because corticosterone levels vary between individuals with respect to their body mass (Kidawa et al. 2014).

To investigate changes in the begging performance after corticosterone implantation, we recorded chicks twice: 1 day before the manipulation and 2 days after the corticosterone implantation. We placed miniature microphones, connected to recorders via a 1-m-long cable, inside the burrows. We set up dictaphone voice recorders (OLYMPUS Recorders) to run for at least 10 h with a sampling rate of 44 kHz. During the Little Auks' breeding period, a polar day provides continuous daylight and parents feed their chicks for 24 h. Chicks often called in the absence of parents, and usually showed increased acoustic activity when one of the parents entered the burrow. The number of feedings registered in the voice recorders was similar during both recording sessions (on average four feedings during 10 h of recordings). In total, we analysed 240 h of recordings using Raven Pro 1.5 (Bioacoustics Research Program 2013). We located the begging sessions (i.e., series of begging calls with a pause not longer than 10 s) visually on spectrograms and waveforms. We measured the length of the begging session (s) and intervals between begging sessions (s) in Raven's waveform and spectrogram views. We calculated the rate of calling (calls per min) within each begging session using Raven's Band Limited Energy Detector (Charif et al. 2010).

In order to compare the growth of corticosterone-implanted (experimental) chicks with that of unmanipulated chicks of the same age (control group), we weighed chicks with an electronic balance (OHAUS, accurate to 0.1 g). We compared the body masses of chicks at the initial stage of

the experiment (3 days after implantation, when chicks were 13–15 days old), prior to chick fledging, as well as the day of life when the chicks left the colony.

### Experiment with parent birds

In the second experiment, we captured adult birds in their nests while brooding their newly hatched chick (1–3 days after the chick hatched). We ringed birds or recorded the ring number for birds already carrying a metal ring. We marked all birds with combinations of colour rings, and colour marks dyed on their breasts, weighed using a PESOLA® balance ( $\pm 1.0$  g), and measured (head-bill length) using callipers ( $\pm 0.1$  mm). The marking patterns enabled the rapid identification of each bird in the field. We chose birds with a similar body mass and similar chick hatching date for the study. We implanted twelve parents (one member of the breeding pair) with corticosterone-releasing pellets (Innovative Research of America, Sarasota, FL, USA; 15 mg corticosterone, 7-day release), in the same way as chicks in the previous experiment. Partners of experimental birds ( $n = 10$ ) and control birds ( $n = 18$ ) underwent the same protocol, but without pellet insertion. Overall, the manipulation lasted for 10–15 min for controls and 15–25 min for experimental birds. We started 24 h continuous observation 48 h after the corticosterone implantation, when we expected the corticosterone boost. Capture, handling, and restraint procedures could affect the stress response in both, experimental and control birds. Moreover, pellet implantation in experimental birds was an additional short-term stressor. We have not used sham incision or placebo pellets here, thus, we are unable to distinguish between the effect of corticosterone pellets and the additional stress made by implantation itself. However, the pellets were continuously releasing a consistent dose of hormone resulting in long-term hormone elevation, while our activities were short-term stressors. Behavioural observations started 48 h after the corticosterone implantation, to allow recovery from manipulation stress. The nest sites of all observed birds were situated in close proximity to each other, to allow observers to monitor the whole colony patch and not to disturb the birds. We monitored the presence of birds continuously and recorded all arrivals with/without food to the nest and departures from the colony. All birds returned to the colony after manipulation.

We measured the body mass of chicks with a corticosterone-implanted parent and control chicks with an electronic balance (OHAUS, accurate to 0.1 g). We compared the body masses in the middle of the nesting period, when chicks were 14–15 days old (the end of the second week of the experiment) and prior to fledging (the end of the fourth week of the experiment).

### Evaluating the corticosterone level after implantation

To monitor corticosterone levels after pellet implantation, we measured the concentration of corticosterone metabolites in faeces, which is a valuable non-invasive method to examine hormone levels and has been successfully validated for Little Auks (Kidawa et al. 2014). We collected faeces immediately in plastic tubes, labelled and maintained in a field cooler box with frozen gel packs for up to 1 h, and then we stored them in a freezer at  $-20$  °C until analysis. During the laboratory analyses, we thawed samples, mixed with 60 % methanol (proportion: 1:10) and vortexed for 30 min (Palme et al. 2013). After centrifugation, we transferred the supernatant to a new tube and used for analysis with an 11-oxoetiocholanolone enzyme immune assay (EIA; for details of the performed EIA see Palme and Möstl 1997; Möstl et al. 2002). We measured faecal corticosterone metabolites in chicks before the manipulation (we obtained the sample just before pellet implantation) and 3 days after corticosterone implantation. We could not monitor the corticosterone level during the initial days after implantation, when we expected the corticosterone boost and made the recordings in the nests, because capture would risk affecting the chicks' begging behaviour. We also collected faecal samples from the control, non-manipulated chicks at a similar age. We did not monitor the corticosterone level in adult birds during the experiment to prevent disturbance to provisioning parents.

### Statistics

We carried out statistical analyses in R 3.2.2 (R Core Team 2015). We applied the two-sample Wilcoxon rank-sum test, also known as the Mann–Whitney test, and the Kruskal–Wallis test when the data did not meet the assumptions of the parametric test (i.e., the level of faecal corticosterone metabolites, body mass measurements in chicks, provisioning rates, and time spent at the colony). For pairwise comparisons we used the Tukey and Kramer (Nemenyi) test with the Tukey-Dist approximation for independent samples (Pohlert 2014).

To compare begging intensity before and after corticosterone manipulation, we analysed the following variables: (1) the number of calls per minute, (2) the length of begging sessions, and (3) the length of intervals between begging sessions with a particular chick as a random effect. We transformed the length of intervals using the Box–Cox method to correct for skewness. We performed analyses using the MCMCglmm package of R software (Hadfield 2010; R Core Team 2015). This test is appropriate for

paired samples, since it recognises repeated measures (before and after treatment) in each chick. Additionally, we performed an extended MCMCglmm analyses: (1) to check whether individual chicks reacted differently to corticosterone manipulation, we added interaction between the random factor (chick) and the fixed factor (experiment); (2) to check whether the effect of the chick was the same before and after manipulation, we added the covariance between the variables. The MCMCglmm analysis uses a Markov chain Monte Carlo (MCMC) estimation approach and is based on the use of Bayesian inference, with prior distributions of unknown parameters. MCMCglmm analysis is one of the few statistical software packages that runs bivariate models to estimate within- and between-individual variance between traits. Bayesian methods, generally referred to as Markov Chain Monte Carlo (MCMC) methods, recently became popular due to developments in computer technology and flexible software programs. We determined the number of iterations, thinning and the burn-in period for our models to improve the effective sample size:  $10^6$  iterations with  $10^5$  burn-in and a thinning interval of  $10^3$ .

## Results

### Experiment with chicks

#### Corticosterone level

Concentrations of faecal corticosterone metabolites in experimental chicks were considerably higher 3 days after implantation than before the manipulation (Kruskal–Wallis test,  $H = 7.2$ ,  $df = 2$ ,  $P = 0.027$ ; Tukey and Kramer post hoc test,  $P = 0.04$ ) or compared to control chicks (Tukey and Kramer post hoc test,  $P = 0.04$ ). Experimental chicks before implantation and control chicks had similar levels of faecal corticosterone metabolites (Tukey and Kramer post hoc test,  $P = 0.97$ ; Table 1). The increase in faecal corticosterone metabolites remained within the physiological range of this species (Kidawa et al. 2014). Chicks implanted with the placebo pellet had similar concentrations before (median = 5.9,  $Q_1$ – $Q_3$ : 4.6–8.9,  $n = 3$ ) and

3 days after implantation (median = 6.89,  $Q_1$ – $Q_3$ : 6.37–10.56,  $n = 3$ ).

#### Begging intensity

The MCMCglmm analyses showed that after the corticosterone implantation, the number of calls per minute by chicks increased significantly (Table 2; Fig. 1). The duration of the begging session before and after the corticosterone manipulation did not differ significantly; however, the intervals between begging sessions were significantly shorter (Tables 3 and 4; Fig. 1). The effect of the chick was weak, but significant, and explained 13 % of the variation (Table 4).

The MCMCglmm analyses for the interaction between the random factor and fixed factor showed that all chicks reacted in the same way to the manipulation (Tables 5, 6, 7 in the “Appendix”). Moreover, MCMCglmm analyses testing the co-variance between the random factor and fixed factor showed that the effect of the chick was the same before and after corticosterone manipulation (Tables 5, 6, 7 in “Appendix”).

#### Chick development

The body mass of control and experimental chicks did not differ at the beginning/initial stage of the experiment (when the chicks were 13–15 days old; Wilcoxon rank-sum test,  $W = 63$ ,  $P = 0.55$ ; Fig. 2). Experimental and control chicks fledged at the same age (median = 25,  $Q_1$ – $Q_3$ : 24–27,  $n = 12$  and median = 25 day,  $Q_1$ – $Q_3$ : 23–25,  $n = 16$ , respectively; Wilcoxon rank-sum test,  $W = 19$ ,  $P = 0.10$ ). However, chicks treated with corticosterone fledged with a significantly higher body mass than control chicks (Wilcoxon rank-sum test,  $W = 31$ ,  $P = 0.002$ ; Fig. 2). All chicks fledged successfully.

### Experiment with parent birds

#### Parental efforts

Experimental and untreated parent Little Auks differed significantly in chick provisioning (Kruskal–Wallis test,

**Table 1** Concentrations of faecal corticosterone metabolites ( $\text{ng g}^{-1}$ ) measured in experimental chicks before the experiment and 3 days after implantation of the corticosterone pellet, and in control chicks

|  | Before implantation |               |     | After implantation |               |     | Control          |               |     |
|--|---------------------|---------------|-----|--------------------|---------------|-----|------------------|---------------|-----|
|  | Median              | $Q_1$ – $Q_3$ | $n$ | Median             | $Q_1$ – $Q_3$ | $n$ | Median           | $Q_1$ – $Q_3$ | $n$ |
| Faecal corticosterone ( $\text{ng g}^{-1}$ ) | 6.1 <sup>a</sup>    | 3.3–11.4      | 10  | 33.3 <sup>b</sup>  | 17.9–49.4     | 7   | 4.5 <sup>a</sup> | 3.3–14.4      | 16  |

Different letters (upper superscript) indicate significant differences between groups

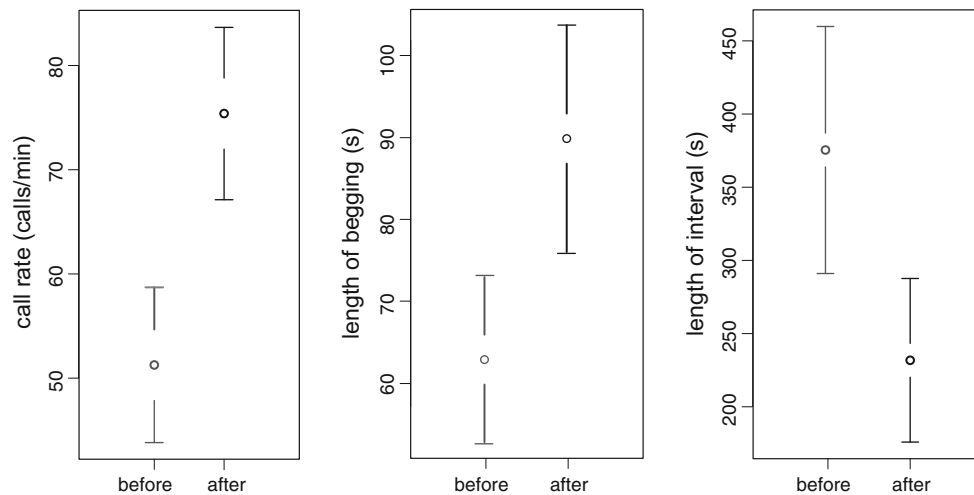


**Table 2** Influence of corticosterone implantation on the call rate (calls/min) with the chick as a random factor analysed using MCMCglmm

|                               | Posterior distribution | Lower 95 % CI          | Upper 95 % CI | pMCMC    |
|-------------------------------|------------------------|------------------------|---------------|----------|
| Fixed terms                   |                        |                        |               |          |
| Call rate after implantation  | 75.89                  | 66.83                  | 85.09         | <0.00001 |
| Call rate before implantation | -23.44                 | -34.91                 | -13.69        | <0.00001 |
| Random term                   |                        |                        |               |          |
| Chick*                        | 62.94                  | $43.68 \times 10^{-6}$ | 213.1         |          |

We compared the call rate in 15 chicks before ( $n = 43$  calls) and after ( $n = 49$  calls) corticosterone implantation

\* The effect of the chick explained 8 % of the variation

**Fig. 1** Begging calls parameters: call rate (*left*), length of begging sessions (*middle*) and length of intervals between begging sessions (*right*) of 15 experimental chicks measured before and after corticosterone implantation (means  $\pm$  confidence intervals)**Table 3** Influence of corticosterone implantation on the length of the begging session (s) with the chick as a random factor analysed using MCMCglmm

|                                    | Posterior distribution | Lower 95 % CI | Upper 95 % CI | pMCMC  |
|------------------------------------|------------------------|---------------|---------------|--------|
| Fixed terms                        |                        |               |               |        |
| Begging length after implantation  | 1.634                  | 1.5076        | 1.7695        | <0.001 |
| Begging length before implantation | -0.004                 | -0.0515       | 0.0407        | 0.896  |
| Random term                        |                        |               |               |        |
| Chick*                             | 0.0436                 | 0.0121        | 0.0931        |        |

We compared the length of the begging sessions in 15 chicks before ( $n = 697$  begging sessions) and after ( $n = 1100$  begging sessions) corticosterone implantation

\* The effect of the chick explained 16 % of the variation

$H = 12.0$ ,  $df = 2$ ,  $P = 0.002$ ). Corticosterone-implanted parents fed the chick significantly less frequently than their untreated partners (Tukey and Kramer post hoc test,  $p = 0.004$ ) and control birds (Tukey and Kramer post hoc test,  $P = 0.016$ ; Fig. 3). We observed no significant differences in feeding frequency between control birds and partners of experimental birds (Tukey and Kramer post hoc test,  $P = 0.601$ ; Fig. 3).

Experimental parents spent less time at the colony (median = 157 min,  $Q_1$ - $Q_3$ : 52–292 min,  $n = 12$ ) than

their partners (median = 282 min,  $Q_1$ - $Q_3$ : 137–425 min,  $n = 10$ ) and control birds (median = 216 min,  $Q_1$ - $Q_3$ : 132–435 min,  $n = 18$ ). However, the differences were not significant (Kruskal–Wallis test,  $H = 2.82$ ,  $df = 2$ ,  $P = 0.24$ ).

#### Chick development

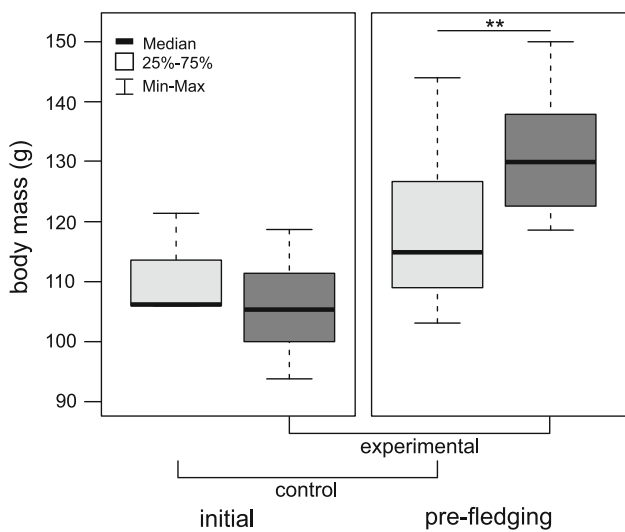
Chicks with a corticosterone-implanted parent attained a significantly lower body mass at the mid stage of the

**Table 4** Influence of corticosterone implantation on the length of interval between the begging sessions (s) with the chick as a random factor analysed using MCMCglmm

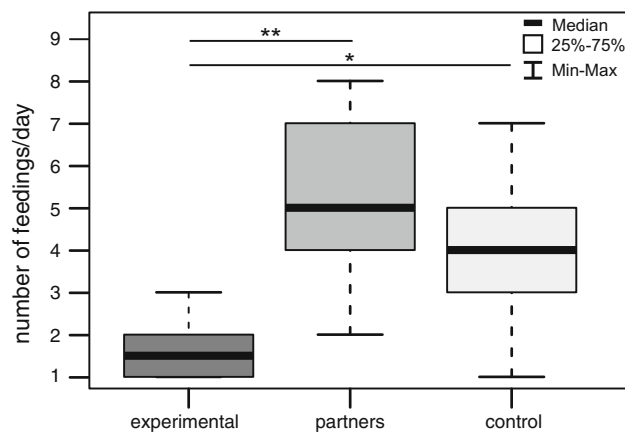
|                                     | Posterior distribution | Lower 95 % CI | Upper 95 % CI | pMCMC  |
|-------------------------------------|------------------------|---------------|---------------|--------|
| <b>Fixed terms</b>                  |                        |               |               |        |
| Interval length after implantation  | 1.914                  | 1.8540        | 1.9678        | <0.001 |
| Interval length before implantation | 0.057                  | 0.0275        | 0.0814        | <0.001 |
| <b>Random term</b>                  |                        |               |               |        |
| Chick*                              | 0.0097                 | 0.0025        | 0.0198        |        |

We compared the length of intervals between the begging sessions in 15 chicks before ( $n = 679$  intervals) and after ( $n = 1089$  intervals) corticosterone implantation

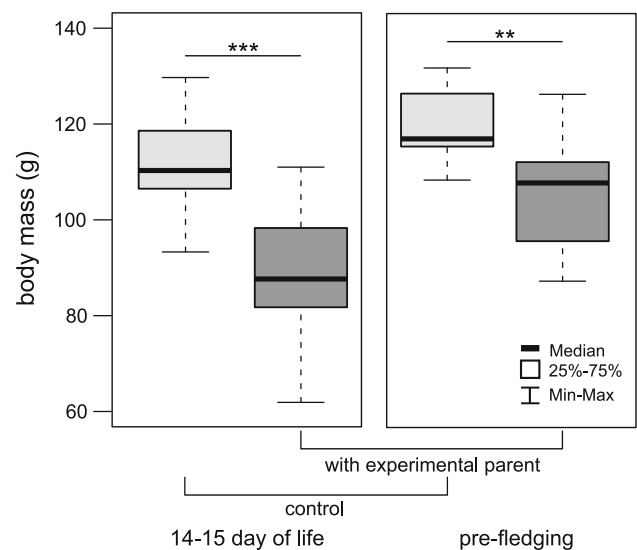
\* The effect of the chick explained 13 % of the variation



**Fig. 2** Body mass of control ( $n = 16$ ) and experimental corticosterone-implanted chicks ( $n = 15$ ). *Left*, chicks at the beginning of the experiment (initial) and *right*, after the experiment (pre-fledging)



**Fig. 3** Number of feedings performed by experimental corticosterone-implanted parent Little Auks ( $n = 12$ ), their partners ( $n = 10$ ) and control birds ( $n = 18$ ) during 24-h continuous observation



**Fig. 4** Body mass of control chicks and chicks with an experimental corticosterone-implanted parent. *Left*, chicks aged 14–15 days ( $n = 20$  control;  $n = 12$  experimental chicks) and *right*, at the pre-fledging stage ( $n = 11$  control;  $n = 11$  experimental chicks)

nesting period (aged 14–15 days; Wilcoxon test,  $W = 212$ ,  $P = 0.0001$ ; Fig. 4) and at the pre-fledging stage (Wilcoxon test,  $W = 101$ ,  $P = 0.007$ ; Fig. 4). Moreover, chicks with a corticosterone-treated parent fledged significantly later than the control chicks (median = 27 day,  $Q_1$ – $Q_3$ : 26–28,  $n = 11$  and median = 25,  $Q_1$ – $Q_3$ : 24–26,  $n = 11$ , respectively; Wilcoxon test,  $W = 27$ ,  $P = 0.026$ ). All chicks fledged successfully.

### Discussion

In this study, we used the main stress hormone in birds, corticosterone, as an experimental factor to simulate the stress reaction and to investigate changes in the behaviour

of Little Auk chicks and parent birds. First, we found that Little Auk chicks intensified their begging performance following corticosterone administration, as the call rates were significantly higher and the intervals between begging sessions were significantly shorter. Due to possible individual differences in begging performance between chicks, we compared the same individuals before and after corticosterone treatment, with the chick as a random factor. In colonially breeding species, the discrimination of their own chicks by parents from other conspecific progeny is biologically important (Penney 1968; Beecher et al. 1981; Falls 1982; Insley et al. 2003). Moreover, Little Auk chicks still rely on parental care after fledging (Stempniewicz 2001); thus, the parent-offspring recognition appears to be essential for chick survival. Indeed, the effect of individual chicks on the begging call parameters was significant, but weak. The detailed analyses of acoustic structure of begging call elements might reveal more specific differences between individuals. However, even if differences in acoustic parameters (i.e., frequency distribution) between individuals exist, they may not play a role in signalling body condition, as it was shown in Thin-billed Prions (Duckworth et al. 2009).

A higher intensity of begging related to an elevated stress hormone concentration provides evidence that begging is an honest signal in Little Auks chicks. The results also suggest that begging calls transmit information concerning the chick's body condition and energy requirements to the parents. A significantly higher pre-fledging body mass of corticosterone-implanted chicks, compared to the control chicks, suggests that parents responded accordingly to the chicks' requirements and provided the chicks with more food. Similarly, increased chick begging rates, together with increased parental food provisioning were observed in chicks of the Black-legged Kittiwake (*Rissa tridactyla*) following an increased corticosterone level (Kitaysky et al. 2001). These results are consistent with those of some previous studies on Little Auks, denoting the ability of parents to increase their feeding frequency (Jakubas et al. 2007; Kwasniewski et al. 2010). It is possible that Little Auks can redirect colony attendance time towards foraging and chick provisioning. However, our experiment with adult birds allowed us to gain insight into how the Little Auks' parental investment decisions may be modified when the parent birds are affected by severe conditions.

In the second experiment, we found that corticosterone-implanted parent Little Auks fed their chicks significantly less frequently than their partners and the control birds. In

consequence, chicks with one experimental parent attained significantly lower body mass and fledged significantly later than chicks of untreated parents. Apart from a reduced chick feeding frequency, experimental parent birds spent slightly more time out of the colony, probably in foraging activity. During the chick-rearing period, Little Auks adopt a bimodal foraging strategy, where they make several short trips (lasting ca 2 h) and then a single long trip (usually lasting >10 h and primarily devoted to self-feeding; Steen et al. 2007; Welcker et al. 2009; Wojczulanis-Jakubas et al. 2010; Welcker et al. 2012). Birds breeding in low-quality foraging habitat perform longer self-feeding trips (even 17–20 h; Welcker et al. 2009; Brown et al. 2012). Accordingly, parent birds with experimentally increased levels of circulating corticosterone presumably made longer self-feeding trips. The length of the long foraging trip and the impact on frequency of short trips could not be ascertained during the 24-h observation period. Nonetheless, a lower provisioning frequency of parents implanted with corticosterone compared to their partners and control birds was evident in our study. Corticosterone orchestrates many physiological and behavioural responses to promote survival, e.g., by mobilizing energy reserves (Axelrod and Reisine 1984; Sapolsky et al. 2000) and increasing locomotor activity (Robin et al. 1998; Landys et al. 2006). Further, the elevated corticosterone levels in parent birds might reduce chick provisioning and even trigger brood desertion (Landys et al. 2006; Angelier et al. 2009). Our results correspond with those of previous studies on Little Auks, which showed that in poor foraging habitat conditions, chick feeding frequency and chick body mass substantially decreased (Harding et al. 2009; Kidawa et al. 2015). A lower body mass has been previously documented in chicks with parents that had their feathers clipped or carried data loggers (Harding et al. 2009; Kidawa et al. 2012). A limitation of our study is the fact that the additional acute stress caused by implanting pellets is indistinguishable from the exogenous corticosterone dissolving from the pellet. Also, we did not consider the possibility of a negative feedback that down-regulates the adrenocortical stress response (Akana et al. 1992; Rich and Romero 2005; Busch et al. 2008). Although we cannot exclude that administration of exogenous corticosterone attenuated the endogenous corticosterone release in response to stress (Akana et al. 1992; Rich and Romero 2005; Busch et al. 2008), a high dose of exogenous corticosterone could replace endogenous corticosterone production (Fusani 2008). Pellet doses used in our study (scaled to the body mass of Little Auks) corresponded to doses, which



successfully increased levels of circulating corticosterone in birds in other experimental studies (Romero et al. 2005; Bourgeon and Raclot 2006; Müller et al. 2009a, b; Spée et al. 2011). Continuous monitoring of corticosterone levels in experimental birds throughout the whole study period would strengthen our conclusions (Fusani 2008). Nonetheless, even a short-term experimental increase of corticosterone level may suppress parental behaviour via reduction of prolactin secretion (Angelier et al. 2009). Marked differences in chick body mass and fledging age between chicks with one experimental parent and chicks of untreated parents confirm reduced parental investment of corticosterone-treated birds over the course of our study.

Some authors have suggested that a reduction in the feeding rate of manipulated birds might be fully or partially compensated for by their non-manipulated partners (Paredes et al. 2005; Harding et al. 2009). Indeed, the results for corticosterone-implanted chicks showed that parents apparently were able to increase provisioning (as reflected in higher mass of corticosterone-implanted chicks at fledging). Nonetheless, in the experiment with corticosterone-implanted parents, we observed no significant increase in the feeding rate of the untreated partner. However, the delivery rate by the partners was one of the highest observed in the studied colony and other Little Auk colonies to date (Stempniewicz and Jezierski 1987; Jakubas et al. 2007; Welcker et al. 2009; Karnovsky et al. 2010; Kwasniewski et al. 2010; Grémillet et al. 2012; Kidawa et al. 2012; Hovinen et al. 2014; Kidawa et al. 2015). It is likely that these birds provisioned chicks at near their maximal rates. Considering the high costs required to sustain themselves (the high cost of flight, foraging and high metabolic rates), Little Auks might often function near to their maximum performance limits. It has been suggested that the flexibility of time and energy budgets of breeding seabirds allows them to adjust food delivery rates according to offspring energy demands, but only when foraging conditions are favourable (Weimerskirch et al. 2001; Litzow and Piatt 2003). For instance, in Common Guillemots, compensation for changes in food quality could occur in a situation in which switching to alternative prey was possible and food quantity was high (Kadin et al. 2016). However, in Little Auks, the foraging efficiency is strongly determined by the quality and not the quantity of available prey species (Kidawa et al. 2015). In contrast to

larger species, small seabirds have fewer reserves to allow their mass to decrease temporarily; thus, their “safety margin for breeding” is relatively low (Duriez et al. 2000). Therefore, we believe that the increase in the chick provisioning rate to compensate for either worse foraging conditions (Jakubas et al. 2007; Kwasniewski et al. 2010) or a reduced feeding rate of the burdened partner (Harding et al. 2009) is possible to some extent; however, it is limited by the birds’ time and energy budget, and greatly depends on the food resources available.

In conclusion, we found that begging constitutes an adaptive mechanism that guards against the decrease in the chicks’ body condition during stressful periods for Little Auks. On the other hand, we do not know whether and to what extent the increased corticosterone level compromises the birds’ future fitness. A nutritional deficit during development can affect the quality of nestlings, which is likely to compromise their cognitive abilities, immune function, and results in increased mortality (Kitaysky et al. 2003, 2006; Loiseau et al. 2008). Therefore, when the fitness costs are higher than the benefits, a reduced parental investment might be adaptive (Angelier et al. 2009). Even though our results suggest that the provisioning rate in long-lived Little Auks can be regulated according to the chick’s needs (expressed by the intensity of the begging display), it appears to be primarily determined by the parents’ body state. The results support the idea that Little Auks will decrease their parental effort and redirect the available energy towards self-maintenance when their energetic state approaches a low threshold.

**Acknowledgments** We wish to thank Lech Stempniewicz and anonymous reviewers for providing valuable comments on the manuscript, Izabela Kulaszewicz for assistance in the field, and Szymon Drobniak for recommending and explaining the MCMCglmm analyses in R. This study was conducted under permits of the Governor of Svalbard and the Norwegian Animal Research Committee. The project was supported financially by the resources from National Science Centre in Poland based on the decision (DEC-2011/01/N/NZ8/04569) and University of Gdańsk (538-L120-B924-15).

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## Appendix

See Tables 5, 6, 7.

**Table 5** Influence of corticosterone implantation on the call rate (no calls/min) with the chick as a random factor analysed using MCMCglmm: (1) with the interaction between the random and the fixed factor; (2) testing the covariance between the variables

|  | Posterior distribution | Lower 95 % CI | Upper 95 % CI | pMCMC  |
|--|------------------------|---------------|---------------|--------|
| (1) Interaction  |                        |               |               |        |
| Call rate after implantation × chick                                 | 0.0668                 | 0.0165        | 0.1422        |        |
| Call rate before implantation × chick                                | 0.0287                 | 0.0033        | 0.0653        |        |
| Interval length after implantation                                   | 1.6489                 | 1.5065        | 1.8047        | <0.001 |
| Interval length before implantation                                  | −0.0396                | −0.2220       | 0.1205        | 0.0622 |
| (2) Covariance   |                        |               |               |        |
| Call rate after implantation: call rate after implantation × chick   | 0.0675                 | 0.0188        | 0.1428        |        |
| Call rate before implantation: call rate after implantation × chick  | 0.0274                 | −0.0061       | 0.0673        |        |
| Call rate after implantation: call rate before implantation × chick  | 0.0274                 | −0.0061       | 0.0673        |        |
| Call rate before implantation: call rate before implantation × chick | 0.0301                 | 0.0030        | 0.0769        |        |
| Interval length after implantation                                   | 1.6498                 | 1.4885        | 1.7957        | <0.001 |
| Interval length before implantation                                  | −0.0346                | −0.1526       | 0.0983        | 0.573  |

We compared the call rate in 15 chicks before ( $n = 43$  calls) and after ( $n = 49$  calls) corticosterone implantation

**Table 6** Influence of corticosterone implantation on the length of the begging session (s) with the chick as a random factor analysed using MCMCglmm: (1) with the interaction between the random and the fixed factor; (2) testing the covariance between the variables

|  | Posterior distribution | Lower 95 % CI | Upper 95 % CI | pMCMC  |
|--|------------------------|---------------|---------------|--------|
| (1) Interaction  |                        |               |               |        |
| Begging length after implantation × chick                                      | 0.0686                 | 0.0195        | 0.1492        |        |
| Begging length before implantation × chick                                     | 0.0288                 | 0.0029        | 0.0727        |        |
| Interval length after implantation   | 1.6493                 | 1.4959        | 1.8047        | <0.001 |
| Interval length before implantation  | −0.0387                | −0.2318       | 0.1426        | 0.664  |
| (2) Covariance   |                        |               |               |        |
| Begging length after implantation: begging length after implantation × chick   | 0.0691                 | 0.0141        | 0.1426        |        |
| Begging length before implantation: begging length after implantation × chick  | 0.0292                 | −0.0018       | 0.0729        |        |
| Begging length after implantation: begging length before implantation × chick  | 0.0292                 | −0.0018       | 0.0729        |        |
| Begging length before implantation: begging length before implantation × chick | 0.0299                 | 0.0039        | 0.0708        |        |
| Interval length after implantation   | 1.6505                 | 1.5066        | 1.8249        | <0.001 |
| Interval length before implantation  | −0.0369                | −0.1655       | 0.1000        | 0.536  |

We compared the length of the begging sessions in 15 chicks before ( $n = 697$  begging sessions) and after ( $n = 1100$  begging sessions) corticosterone implantation

**Table 7** Influence of corticosterone implantation on the length of interval between the begging sessions (s) with chick as a random factor analysed using MCMCgmm: (1) with the interaction between the random and the fixed factor; (2) testing the covariance between the variables

|  | Posterior distribution | Lower 95 % CI | Upper 95 % CI | pMCMC  |
|--|------------------------|---------------|---------------|--------|
| (1) Interaction  |                        |               |               |        |
| Interval length after implantation × chick                                       | 0.0095                 | 0.0020        | 0.0207        |        |
| Interval length before implantation × chick                                      | 0.0131                 | 0.0030        | 0.0297        |        |
| Interval length after implantation   | 1.9180                 | 1.8567        | 1.9750        | <0.001 |
| Interval length before implantation  | 0.0650                 | −0.0227       | 0.1579        | 0.158  |
| (2) Covariance   |                        |               |               |        |
| Interval length after implantation: interval length after implantation × chick   | 0.0093                 | 0.0025        | 0.0199        |        |
| Interval length before implantation: interval length after implantation × chick  | 0.0066                 | −0.0014       | 0.0163        |        |
| Interval length after implantation: interval length before implantation × chick  | 0.0066                 | −0.0013       | 0.0163        |        |
| Interval length before implantation: interval length before implantation × chick | 0.0129                 | 0.0029        | 0.0276        |        |
| Interval length after implantation   | 1.9155                 | 1.8658        | 1.9769        | <0.001 |
| Interval length before implantation  | 0.0668                 | 0.0106        | 0.1380        | 0.042  |

We compared the length of intervals between the begging sessions in 15 chicks before ( $n = 679$  intervals) and after ( $n = 1089$  intervals) corticosterone implantation

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