



Robertson, G. S., Bolton, M., and Monaghan, P. (2015) Parental resource allocation among offspring varies with increasing brood age in Black-legged Kittiwakes *Rissa tridactyla*. *Bird Study*

Copyright © 2015 The Authors

<http://eprints.gla.ac.uk/101024/>

Deposited on: 18 May 2015

Enlighten – Research publications by members of the University of Glasgow  
<http://eprints.gla.ac.uk>

# Parental resource allocation among offspring varies with increasing brood age in Black-legged Kittiwakes *Rissa tridactyla*

GAIL S. ROBERTSON<sup>1\*</sup>, MARK BOLTON<sup>2</sup> and PAT MONAGHAN<sup>1</sup>

<sup>1</sup>Institute of Biodiversity, Animal Health and Comparative Medicine, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK; <sup>2</sup>RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire SG19 2DL, UK

**Capsule** Black-legged Kittiwakes *Rissa tridactyla* breeding at a North Sea colony allocated more resources to younger chicks with increasing brood age.

**Aims** Examine how feeding, attendance and resource allocation change with increasing brood age and how allocation of feeds affects growth rate and fledging success.

**Methods** Broods of two were observed on Coquet Island to compare feeding rates and fledging success between chicks of different hatching order.

**Results** Growth and feeding rates were similar between chicks of different hatching order. The relationship between growth and feeding rate may have differed between siblings, although this relationship was not strong. Feeding rate per brood and nest attendance decreased nonlinearly as brood age increased. First-hatched chicks were fed more frequently at the beginning of multiple feeds and received a higher proportion of feeds during early chick-rearing. However, during late chick-rearing second-hatched chicks received proportionally more feeds.

**Conclusion** Parents reduced overall feeding rate as brood age increased, while increasing the proportion of resources allocated to younger offspring. This may explain general similarities in growth rate and fledging success between chicks of different hatching order. By considering resource allocation throughout development we can better understand parental investment strategies in asynchronous species.

Iteroparous individuals balance allocation of limited resources among offspring during a reproductive event (Royle *et al.* 2002, 2004). Parental allocation decisions vary depending on number of offspring (Rogowitz & McClure 1995, Rogowitz 1996), parental condition (Tveraa *et al.* 1998) and resource availability (Braun & Hunt 1983, Erikstad *et al.* 1998). Allocation decisions may be expected to vary throughout the developmental period as offspring demand and foraging conditions change (Tveraa *et al.* 1998, Granadeiro *et al.* 2000).

Theoretical models predict that parents should invest more resources in offspring with the greatest need, usually the smallest (Godfray 1995). While some studies have shown that older offspring tend to solicit food from parents more frequently than younger chicks

(Drummond 2002, Royle *et al.* 2002), others have reported that parents consistently feed larger offspring more often than their smaller siblings, even when not signalling the greatest need (Price & Ydenberg 1995, Price *et al.* 1996). In bird species with asynchronously hatching young, parents preferentially allocate resources to older, larger chicks, which are of higher value to parents than younger offspring that are less likely to survive to fledging (Parker *et al.* 2002). First-hatched chicks in asynchronous broods are generally larger than second-hatched chicks and are fed at a higher rate (Braun & Hunt 1983, Price & Ydenberg 1995, Royle *et al.* 2012). As feeding rate is generally positively correlated with growth rate (Braun & Hunt 1983, Donazar & Ceballos 1989), older chicks may be expected to have higher growth rates and therefore be more likely to survive to fledging than younger chicks (Hahn 1981, Kersten & Brenninkmeijer 1995, Stienen

\*Correspondence author. Present address: Game and Wildlife Conservation Trust, Uplands Research, Eggleston, Barnard Castle, Co. Durham DL12 0AG, UK. Email: [gsrobertson4@gmail.com](mailto:gsrobertson4@gmail.com)

& Brenninkmeijer 2006, Royle *et al.* 2012, Merklings *et al.* 2014).

It is difficult to predict how parental resource allocation will vary with offspring age. Increasing reproductive value of offspring over time should favour an increase in parental investment, while reduction in the beneficial effects of parental care on offspring survival and increasing requirements of parents to replenish their own depleted resources are likely to favour a reduction (Sargent & Gross 1986, Redondo & Carranza 1989, Pugesek 1990). Studies on birds have shown that parents match feeding rates to increasing chick energy requirements over time (Ricklefs *et al.* 1985, Bertram *et al.* 1991). The energy demands of chicks peak at the period of maximum growth (Ricklefs & White 1981) hence chicks generally require more food during maximum growth and less as they approach fledging age (Cairns 1987, Emms & Verbeek 1991, Roby 1991). Adults usually decrease the amount of energy delivered to chicks prior to fledging (Cairns 1987, Emms & Verbeek 1991), either to match declining energy demands of chicks or as a strategy to induce fledging (Emms & Verbeek 1991, Roby 1991). Hence, parental investment, as quantified by food delivery rate, may be expected to vary throughout the chick developmental period as energetic demands of offspring change.

Previous studies on seabird species, including Kittiwakes, have shown that adult nest attendance declines over the course of chick development (Coulson & Johnson 1993, Cadiou & Monnat 1996, Chiaradia & Kerry 1999). Parents are likely to reduce nest attendance as chick demand for food increases, while their vulnerability to predation decreases (Gaston & Nettleship 1982, Davies & McCaffrey 1986, Coulson & Johnson 1993). These changes stimulate parents to devote more time to foraging and to spend less time at the nest (Lewis *et al.* 2004). However, the age at which chicks are first left alone at the nest varies depending on food availability around the breeding colony (Hamer *et al.* 1993).

As timing of maximum growth and peak energy demand varies among offspring of different hatching order (Drent & Daan 1980, Mock & Schwagmeyer 1990), and as reproductive value of offspring increases with age (Redondo & Carranza 1989), parents may be expected to increase the proportion of resources allocated to younger chicks in a brood later in the developmental period (Kloskowski 2001, Shizuka & Lyon 2009). It has been previously shown that greater cooperation among siblings can be expected later in

development as energy demands decline (O'Connor 1978, Kloskowski 2001). While resource allocation between parents and offspring and among offspring have been examined in several species (Ricklefs 1987, Jodice *et al.* 2002, Royle *et al.* 2002), fewer studies have examined how food distribution varies among offspring throughout the developmental period and how this affects reproductive success (but see Seddon & van Heezik 1991, Kloskowski 2001, Shizuka & Lyon 2009). We expect the proportion of total resources allocated to second-hatched chicks to increase with brood age, and as the first few feeds delivered by a returning adult are generally larger and likely to contain more energy than subsequent feeds (Anderson & Ricklefs 1992), we expect first-hatched chicks to initially receive the first feed in a multiple feed bout more frequently than second-hatched chicks, but for second-hatched chicks to receive the first feed more often as brood age increases.

We investigated intra-brood parental resource allocation in two-chick broods of Black-legged Kittiwakes *Rissa tridactyla* (hereafter 'Kittiwake') on Coquet Island, northeast England. We predict: (1) first-hatched chicks to be fed more frequently and have higher growth rates and fledging success than second-hatched chicks; (2) parental feeding and nest attendance to increase until chicks reach maximum growth and decrease as they approach fledging age; (3) parents to allocate a greater proportion of resources to second-hatched chicks as brood age increases. We discuss how our results contribute to the understanding of parental resource allocation in species with asynchronously hatching offspring.

## METHODS

### Study site

The study took place on Coquet Island, northeast England (55°20'N, 1°32'W) during the chick-rearing period from June to July 2012. Coquet Island is a small (5 ha) island, 2 km from the mainland coast and is managed for seabirds by the Royal Society for Protection of Birds (RSPB). Kittiwakes established a breeding colony on Coquet in 1991 after substantial numbers visited in 1990 (Coulson & Coulson 2008). The colony then expanded to 215 pairs in 2012. Permission to carry out research on Coquet was granted by Natural England.

Kittiwakes are a suitable species in which to examine parental resource allocation because they are easy to

observe on breeding cliffs and, provided due care is taken, allow close approach without causing disturbance which would affect breeding success (Sandvik & Barrett 2001, Brewer *et al.* 2008). Each nest is a separate structure from which chicks generally do not stray until a few days prior to fledging allowing observations of individual broods to be made (Galbraith 1983). Feeding rate and trip duration can be deduced for large numbers of nests through colony observations. Mean trip duration is relatively short for Kittiwakes foraging during chick-rearing (mean  $\pm$  se =  $2.87 \pm 0.53$  hours for 13 birds tracked on Coquet Island during mid-chick-rearing in 2012; Robertson *et al.* 2014). Hence, numerous nest deliveries can be recorded during a few hours of observation. Mean trip duration of birds in this study was estimated to be  $1.08 \pm 0.06$  hours, probably due to prey availability close to the breeding colony in June–July.

Kittiwake broods vary in size from 1–3 chicks (Coulson 2011), depending on parental body condition, breeding experience and food availability (Coulson & White 1961, Coulson & Porter 1985, Jacobsen *et al.* 1995). In our study, the majority of pairs had broods of two: broods of three and single broods (either from single clutches or from broods which lost chicks during the study period) were excluded from analyses (a total of nine nests). Chicks close to fledging would occasionally leave the nest during observations towards the end of the developmental period, leaving a single chick in the nest. While these chicks invariably returned before subsequent observations, occasions when one chick was at the nest were excluded from analyses. This avoided bias when comparing proportion of feeds allocated by parents to chicks of different hatching orders.

### Nest observations

To produce an adequate sample size for analyses, 30 study nests were selected from an area close to the centre of the Kittiwake colony by assigning a unique number to each nest and using a random number generator (R version 3.0.1) to randomly select nests. The position of nests within Kittiwake colonies has been shown to affect reproductive success and survival; nests towards the centre of colonies tend to have higher fledging success than those at the edge (Coulson & Thomas 1985, Aebischer & Coulson 1990). To examine how parental feeding rate and

intra-brood resource allocation varied with increasing brood age, we selected study nests at the centre of the colony that were likely to maintain broods of two throughout the chick developmental period. Hence, nests positioned at the edge of the colony, and those difficult to reach for the purpose of marking chicks, were excluded from the selection process. The former condition is likely to mean that we excluded young and possibly low-quality pairs from this study. Study nests were checked every 2–3 days allowing the hatching date of each chick to be recorded. First-hatched (A) chicks ( $n = 21$ ) hatched  $\sim 0.89 \pm 0.22$  (mean  $\pm$  se) days before second-hatched (B) chicks ( $n = 21$ ), and were  $10.4 \pm 4.8$  g heavier than second-hatched chicks weighed at the same age. Approximately 2–4 days after hatching, A chicks in each nest were marked using a small amount of water-soluble non-toxic Tippex<sup>®</sup> on the tip of the beak which was clearly visible from the ground using binoculars ( $8 \times 10$  magnification) (Cook *et al.* 2000, Skórka *et al.* 2012).

Observations of study nests took place from a portable hide positioned  $\sim 10$ – $15$  m from the base of cliffs (maximum distance at which chicks could be conclusively identified). Hatching dates were relatively synchronous (6–13 June) hence chicks were of similar ages when observations began (4–10 days old). Study nests were observed from 17 June–17 July 2012 for 1–2 watches per day. Watches were carried out for three hours and care was taken to include every time period from 0400 to 2100 hours for each tidal state (low, high, rising and falling). The start time for daily observations varied depending on tidal conditions. For each nest, we recorded time of arrival of an adult with food, time of departure of either adult, whether or not an adult was attending the nest when its partner returned with food, which chick was fed during feeding bouts, how many times an adult regurgitated food to each chick and the order in which chicks were fed during multiple feed bouts. Trip duration was quantified by recording the time of adult departure and return to the nest during each observation period. Although adults were not marked, trip duration prior to food delivery could be deduced on occasions when an adult was recorded leaving the nest and returning to feed at least one chick while the second member of the pair continuously attended the nest. Trip duration could not be deduced on occasions when both adults were absent from the nest simultaneously. Mean trip duration calculated from GPS-tracked birds at the same colony was  $< 3$  hours

(Robertson *et al.* 2014), which suggests that three-hour observation periods can be used to record whole foraging trips.

### Data analyses

A feed was defined as an occasion during which an adult regurgitated food to a chick. A feeding bout was defined as a period during which either attending adults or those returning to the nest from a foraging trip delivered food on one or more occasions to at least one chick in a brood. Adults began feeding chicks within 15 minutes of returning to the nest which was also the maximum time period for which an adult was observed continually feeding chicks during a feeding bout (G.S. Robertson, pers. obs.). Hence, separate feeding bouts were regarded as those where chick feeds occurred >15 minutes apart. Feeding bouts which began within 15 minutes of the end of an observation period were excluded from analyses. A total of 686 feeding bouts were recorded from the 30 nests over a total of 135 hours of observations.

Kittiwakes deliver meals to chicks by regurgitating food stored in a crop hence adults can make multiple regurgitations while feeding chicks (Coulson 2011). A multiple feed bout refers to feeding bouts during which an adult regurgitated food more than once to at least one chick within 15 minutes of the first initial feed. The order in which A and B chicks were fed during a multiple feed bout was recorded and the number of bouts in which B chicks were fed first was expressed as a proportion of the total number of bouts. To compare the number of feeds allocated to A and B chicks during both single and multiple feed bouts, the number of feeds received by the B chick in a brood was expressed as a proportion of the total number of feeds delivered to both chicks.

Two metrics of feeding rate were calculated, one to examine how the number of feeds delivered to each chick per hour differed between chicks of different hatching order and how this affected growth rate (total feeding rate per chick, hereafter 'chick feeding rate'), and another to determine how number of feeds delivered to each brood per hour varied with increasing brood age (hourly feeding rate per brood, hereafter 'brood feeding rate'). Chick feeding rate was calculated by dividing the total number of times a chick received food from an adult during the linear growth phase by the total number of hours for which that chick was observed. Brood feeding rate was defined as the number of feeds delivered to each brood

per hour of observation throughout the developmental period.

In order to limit disturbance to the colony, chick weights were recorded on only two occasions during the linear growth phase (Coulson & Porter 1985). Each chick in a study nest was weighed twice to the nearest 0.1 g using electronic scales (SATRUE SA-500), first when chicks were 2–8 days old and again when the same chicks were 16–20 days old. A and B chicks from the same brood were weighed as close together in time as possible, usually on the same day during the same nest visit. Chick growth rate ( $\text{g day}^{-1}$ ) was calculated for each chick using the following equation (Coulson & Porter 1985, Nisbet *et al.* 1995):

$$\text{Chick growth rate} = \frac{W_2 - W_1}{D_2 - D_1},$$

where  $W_1$  is the weight (g) at first measurement ( $2 \leq$  chick age  $\leq 8$  days old),  $W_2$  is the weight (g) at second measurement ( $16 \leq$  chick age  $\leq 20$  days old),  $D_1$  is the date of first measurement and  $D_2$  is the date of second measurement.

Growth rate and chick feeding rate were both calculated during the linear growth phase. Chick skeletal measurements (such as tarsus and wing length) were not recorded in this study to reduce chick handling time and disturbance to the colony. Previous studies have also calculated chick growth rate using weight measurements recorded during the linear growth phase (Coulson & Porter 1985, Coulson & Thomas 1985). Fledging success (%) was calculated as the percentage of hatched chicks observed leaving the nest at the end of the developmental period (Spahn & Sherry 1999). Unless otherwise stated, linear mixed models (LMMs) used in analyses were fitted with normal error distributions and identity link functions, and included nest ID as a random factor.

LMMs were used to examine whether A chicks were fed more frequently and had higher growth rates and fledging success than B chicks (our first hypothesis outlined above), by comparing growth rates and chick feeding rates of chicks of different hatching order, and by examining how much variation in growth rate could be explained by chick feeding rate.

Our second hypothesis, that parental feeding and attendance will increase until chicks reach maximum growth and decrease thereafter, was tested by examining variation in brood feeding rate, trip duration and nest attendance (whether or not study



necks were already attended by a parent each time an adult returned to the nest to feed at least one chick) with increasing brood age. Brood age (in days after hatching) was defined as the difference between the date on which an observation was made and date of first hatching within a brood. Variation in brood feeding rate and trip duration with increasing brood age (expressed as a continuous variable from 0 to ~40 days old) were examined using LMMs, while changes in nest attendance with increasing brood age were examined using a generalized linear mixed model (GLMM) with a binomial error distribution. GLMMs used the logit link function and included nest ID as a random factor unless otherwise stated.

Our third hypothesis, that parents will allocate a greater proportion of resources to second-hatched chicks as brood age increases, was tested by examining variation in the proportion of total feeds delivered to a brood received by B chicks, during both single and multiple feed bouts, using a GLMM with a binomial error distribution (where the response variable was the proportion of total feeds received by B chicks during single and multiple feed bouts). A GLMM with a binomial error distribution was used to examine variation in the probability that first feeds were allocated to B chicks during multiple feed bouts throughout the chick-rearing period (where the response variable was whether a given first feed was received by a B chick (1) or an A chick (0)).

For each LMM and GLMM, we first fitted a fully parameterized model using maximum likelihood and removed terms by sequential deletion while testing for significant changes in model variance using likelihood ratio tests (LRTs) (Crawley 2007). We then refitted the minimum adequate model using restricted maximum likelihood (REML) to estimate effect sizes. Where necessary, brood feeding rate was log-transformed to reduce heteroscedasticity in the residuals and improve the fit of the model. To confirm that model assumptions were adhered to, residuals were tested for normality and homoscedasticity by examining histograms of the residuals and residual versus fitted plots. Receiver operating characteristic (ROC) curves and associated area under the curves (AUC) were used to examine the fit of binomial GLMMs. ROC curves are obtained by plotting the fraction of 'true positive' values against the fraction of 'false positive' values predicted by the model (Fielding & Bell 1997). AUC (a value between 0.5 and 1.0) provides a measure of model accuracy, where values close to 0.5 indicate that fractions of true positive and

false positive values predicted by the model are similar and that the model only predicts a true positive value 50% of the time, while values of 1.0 indicate that the model correctly predicts a true positive value 100% of the time (Fielding & Bell 1997). AUC values of 0.5–0.7 indicate low model accuracy, while values >0.9 indicate high model accuracy (Pearce & Ferrier 2000). LMMs and GLMMs were fitted using the 'lme4' R package (Bates *et al.* 2014). Analyses were carried out in R version 3.1.2 (R Core Development Team 2014). Means are presented  $\pm$ se throughout.

## RESULTS

### Effect of differential resource allocation on growth rate and fledging success

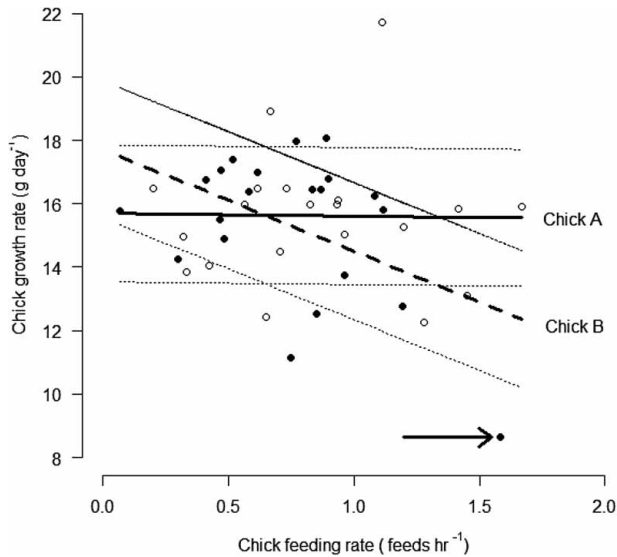
There was no significant difference between chick feeding rates (in feeds hour<sup>-1</sup>) calculated during the linear growth phase for A and B chicks ( $0.85 \pm 0.09$  and  $0.75 \pm 0.08$ , respectively; LMM:  $\chi^2_1 = 2.3$ ,  $P = 0.13$ ,  $n = 42$ ) and no difference between growth rates (g day<sup>-1</sup>) of chicks of different hatching order ( $15.62 \pm 0.46$  and  $15.31 \pm 0.52$  for A and B chicks, respectively; LMM:  $\chi^2_1 = 0.4$ ,  $P = 0.53$ ,  $n = 42$ ).

A two-way interaction between chick feeding rate and chick hatching order explained a significant amount of variation in growth rate ( $\chi^2_1 = 5.3$ ,  $P = 0.02$ ,  $n = 42$ ) and for B chicks, growth rate declined with increasing feeding rate (Table 1, Fig. 1). However, Fig. 1 suggests that the significance of this interaction was influenced by one B chick data point. When this analysis was repeated excluding this data point no significant interaction between chick feeding rate and hatching

**Table 1.** Results of LRTs from an LMM with a normal distribution and identity link function examining the effect of chick feeding rate (feeds hour<sup>-1</sup>) and hatching order on chick growth rate (g day<sup>-1</sup>). Output from a minimum adequate model fitted using REML is displayed. Random factor = nest ID ( $n = 21$  nests).  $n = 42$  chicks.

Variable removed	$\chi^2$	df	P
Chick feeding rate	1.8	1	0.17
Hatching order	0.8	1	0.37
Chick feeding rate $\times$ Hatching order	5.3	1	0.02
Minimum adequate model	Estimate	se	
Intercept	15.70	1.05	
Chick feeding rate	-0.08	1.10	
Hatching order	2.02	1.18	
Chick feeding rate $\times$ Hatching order	-3.13	1.37	

Values displayed for hatching order are given relative to first-hatched chicks.

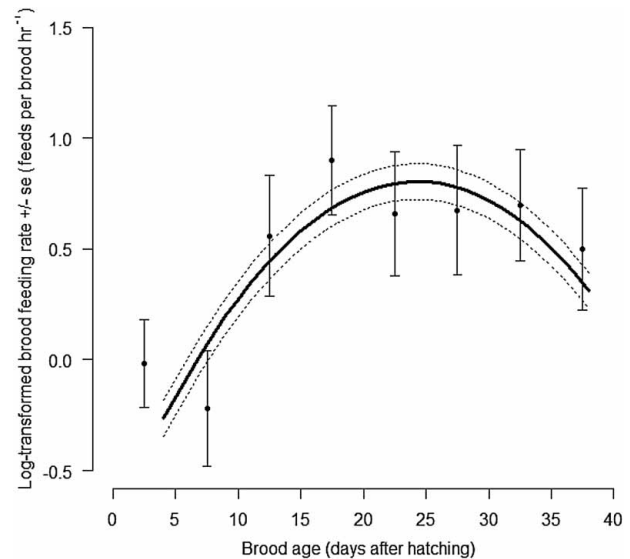


**Figure 1.** Relationship between chick growth rate ( $\text{g day}^{-1}$ ) and chick feeding rate ( $\text{feeds hour}^{-1}$ ) during the linear growth phase for chicks of different hatching order. Straight lines were fitted using coefficients estimated from an LMM with a normal error distribution. The solid line represents the relationship between chick growth rate and feeding rate for A chicks (open circles), and the dashed line represents the same relationship for B chicks (filled circles). The dotted lines represent standard errors of predicted lines for each hatching order. The arrow highlights the B chick data point which determines the significance of the interaction.

order was found ( $\chi^2_1 = 1.3$ ,  $P = 0.26$ ,  $n = 41$ ). However, as there was no obvious biological reason to exclude data collected from the B chick or its brood from the analysis, the data point was retained. Overall fledging success of study nests was high (87.1%), and only a slightly higher percentage of A chicks from study nests survived to fledge (93.3%) than B chicks (89.7%). A chi-squared test comparing the fledging success of chicks of different hatching order showed there to be no significant difference between fledging success of A and B chicks ( $\chi^2_1 = 0.002$ ,  $P = 0.97$ ). Overall fledging success of study nests was very high, which may be because we selected nests only from the centre of the colony, which were likely to maintain a brood size of two throughout the chick development period.

### Variation in parental feeding and nest attendance with increasing brood age

Brood feeding rate increased slowly with brood age before declining as chicks approached fledging (Fig. 2). Due to the quadratic relationship between brood feeding rate and brood age, brood age squared was



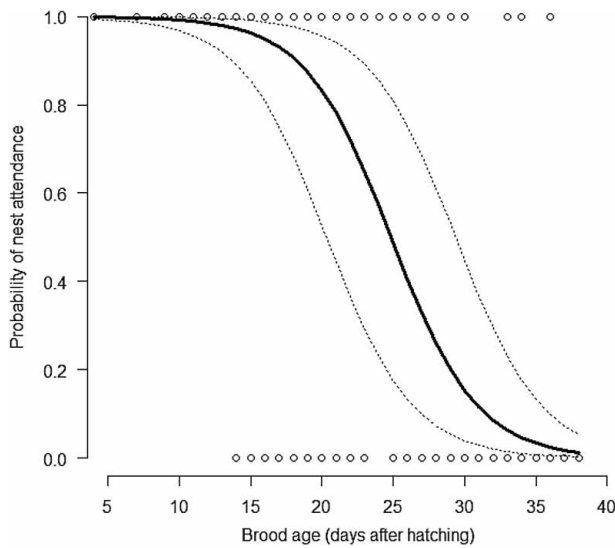
**Figure 2.** Relationship between log-transformed brood feeding rate ( $\text{feeds per brood hour}^{-1}$ ) and brood age (days after hatching). Mean log-transformed brood feeding rate  $\pm$  se was calculated for each five-day brood age category. The curved line was fitted using coefficients from an LMM with normal error distribution. The dashed lines represent standard errors around the fitted line.

**Table 2.** Results of LRTs from an LMM with a normal distribution and identity link function examining the effect of increasing brood age on  $\log(\text{brood feeding rate})$  ( $\text{feeds per brood hour}^{-1}$ ). Output from a minimum adequate model fitted using REML is displayed. Random factor = nest ID ( $n = 21$  nests).  $n = 483$  observations.

Variable removed	$\chi^2$	df	$P$
Brood age	29.4	1	<0.001
Brood age <sup>2</sup>	25.1	1	<0.001
Minimum adequate model	Estimate	se	
Intercept	-0.73	0.24	
Brood age	0.13	0.02	
Brood age <sup>2</sup>	-0.003	0.0005	

included in an LMM examining how feeding rate changes with increasing age. Both brood age and brood age squared explained a significant amount of variation in feeding rate (Table 2).

Nest attendance varied nonlinearly with increasing brood age, declining as brood age increased (Fig. 3). A GLMM with a binomial error distribution was used to examine the relationship between change in nest attendance and brood age, where an occasion when a parent attended a nest was defined as 1, and occasions when a nest was unattended was defined as 0. Brood age was found to have a significant



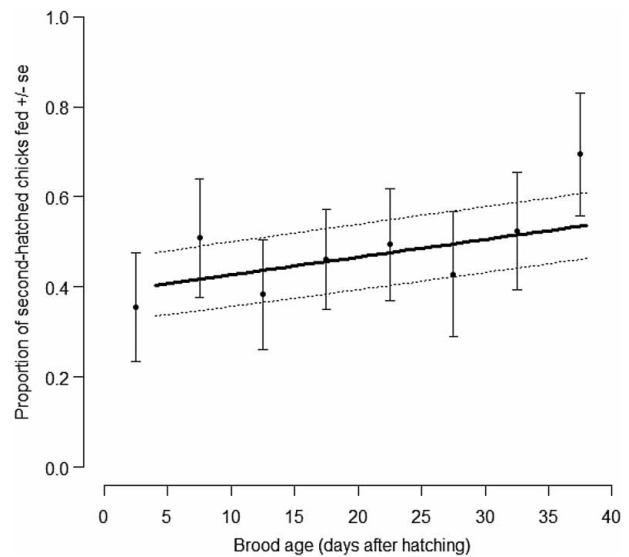
**Figure 3.** Relationship between probability of a nest being attended when an adult returned with food and brood age (days after hatching) for broods aged 4–38 days old. The curved line was fitted using coefficients estimated from a GLMM with binomial error distribution and a logit link function, the dashed lines represent standard errors around the fitted line.

negative effect on the probability of a nest being attended by a parent when an adult returned with food and attendance declined as brood age increased ( $\chi^2_1 = 275.9$ ,  $P < 0.001$ ,  $n = 446$ ; Estimate  $\pm$  se =  $-0.33 \pm 0.03$ ; AUC = 0.93). An LMM with a normal error distribution and identity link function was used to examine how trip duration varied with increasing brood age. The model showed that there was no effect of increasing brood age on parental foraging trip duration ( $\chi^2_1 = 0.1$ ,  $P = 0.81$ ,  $n = 79$ ).

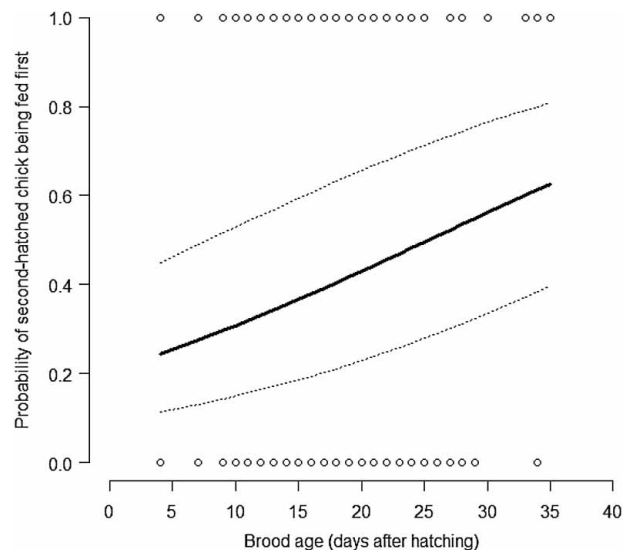
**Variation in intra-brood resource allocation with increasing brood age**

A GLMM with a binomial error distribution showed that the proportion of total feeds received by B chicks, during single and multiple feed bouts, increased with increasing brood age ( $\chi^2_1 = 6.4$ ,  $P = 0.01$ ,  $n = 446$ ; Estimate  $\pm$  se =  $0.02 \pm 0.01$ ; AUC = 0.94; Fig. 4).

Variation in the probability of first feeds from multiple feed bouts being allocated to B chicks with increasing brood age was examined using a GLMM with a binomial error distribution. The probability of B chicks being fed first was found to increase significantly with brood age ( $\chi^2_1 = 5.0$ ,  $P = 0.03$ ,  $n = 190$ ; Estimate  $\pm$  se =  $0.05 \pm 0.02$ ; AUC = 0.94; Fig. 5).



**Figure 4.** Relationship between the proportion of second-hatched chicks which were fed during both single and multiple feed bouts and brood age (days after hatching). Mean proportion of occasions when second-hatched chicks were fed  $\pm$  se was plotted for each five-day brood age category. The line was fitted using coefficients estimated from a GLMM with binomial error distribution and a logit link function. The dashed lines represent standard errors around the fitted line.



**Figure 5.** Relationship between the probability of second-hatched chicks being fed first during multiple feed bouts and brood age (days after hatching). The curved line was fitted using coefficients estimated from a GLMM with binomial error distribution and a logit link function. The dashed lines represent standard errors around the fitted line.



## DISCUSSION

Asynchronous hatching has been observed in different bird species, including Kittiwakes (Braun & Hunt 1983, Magrath 1990, Stenning 1996). It has been suggested that asynchronous hatching is a strategy to induce brood reduction during periods of food shortage by producing a competitive hierarchy within broods (Lack 1947, 1954, Ricklefs 1965, Merklings *et al.* 2014). However, some evidence suggests that external drivers such as predation risk, temperature control and embryo viability introduce brood hierarchy (Clark & Wilson 1981, Stenning 1996, Hillström *et al.* 2000), although evidence for this is not as strong.

While previous studies have shown that first-hatched Kittiwake chicks tend to receive food from parents significantly more frequently than younger offspring (Braun & Hunt 1983, White *et al.* 2010), we found no significant difference in the feeding or growth rates of A and B chicks during the linear growth phase. This is contrary to what we initially expected, although other studies have also reported no effect of hatching order on feeding rates (Merklings *et al.* 2014). Our results may have been influenced by extremely high food availability in the area surrounding the colony in 2012.

Kittiwakes are facultatively siblicidal birds, and aggressive interactions frequently occur among brood mates (White *et al.* 2010, Coulson 2011). Aggression is more common during periods of low food availability (White *et al.* 2010), hence high food abundance may explain why few incidences of physical conflict between siblings were observed in our study. Because we did not observe study nests for long continual periods, it is possible that occasions of aggression were missed.

Although there were no available data on prey abundance around Coquet Island in the year of our study, productivity of the whole colony was generally high (number of chicks fledged per nest = 1.2 (taken from a random sample of 30 nests); productivity range on Coquet Island 1991–2011 = 0.4–2.0; [www.jncc.defra.gov.uk/page-4460](http://www.jncc.defra.gov.uk/page-4460)) when compared with other colonies and years (productivity = 0.02–0.97 chicks per nest on the Isle of May, southeast Scotland; Lewis *et al.* 2001; mean productivity 1986–2004 for colonies in east England = 1.02 chicks per nest; Frederiksen *et al.* 2007). Trip duration of birds in our study was short which suggests that prey were available close to the colony (Monaghan *et al.* 1994, Croxall *et al.* 1999). Also, fledging success of both A and B chicks was very high, considerably higher than fledging success in previous studies, indicative of an extremely

good feeding environment (Cairns 1988, Murphy *et al.* 1991, Gill *et al.* 2002, Coulson 2011), which may have influenced our results. However, our sample of study nests may be biased because we selected nests from the centre of the colony, which have been shown to have higher fledging success than nests positioned at the colony edge (Coulson & Thomas 1985, Aebischer & Coulson 1990).

Although we found growth rate to be comparable for chicks of different hatching order, there was a significant negative relationship between growth rate and chick feeding rate for B chicks, while no relationship was evident for A chicks. B chicks with high feeding rates appeared to have significantly lower growth rates than A chicks fed at the same rate, although this relationship was weak and was largely driven by one data point. Other studies have suggested that the size and energy content of regurgitates fed to chicks varies depending on hatching order, and that younger chicks receive less energy per regurgitate than older chicks (Galbraith 1983, Golet *et al.* 2000). While we were unable to regularly collect regurgitate samples due to imposed limits to colony disturbance on Coquet Island, it seems possible that variation in regurgitate content may explain why B chicks with high feeding rates may have had significantly lower growth rates than A chicks fed at the same rate.

Parental resource allocation may be expected to vary throughout the developmental period in response to changing offspring energy requirements and environmental conditions (Ricklefs *et al.* 1985, Emms & Verbeek 1991, Low *et al.* 2012). While increasing reproductive value of offspring with age should favour an increase in parental feeding and attendance, reductions in the benefit of parental care and the increasing requirement of parents to replenish depleted resources later in the breeding season may favour a reduction (Sargent & Gross 1986, Redondo & Carranza 1989, Pugsek 1990). In our study both brood feeding rate and nest attendance changed nonlinearly with increasing brood age. Brood feeding rate increased until chicks were 21–25 days old, before declining as chicks approached fledging age at 30–40 days old (Maunder & Threlfall 1972, Coulson 2011). Merklings *et al.* (2014) found the reverse to be true; feeding rates decreased with increasing chick age for chicks  $\leq 20$  days old. Because we found no change in trip duration with increasing brood age, the decrease in feeding rate we observed for chicks >21–25 days old may have been due to parents retaining more food when broods were older, or delivering larger meals to older broods.

There was no change in parental foraging trip duration with increasing brood age, which suggests that food availability remained adequate throughout the chick-rearing period because parents showed no increase in foraging effort later in the breeding season (Abrams 1991, Petersen *et al.* 2006). It may be that a decline in feeding rates later in the breeding season reflects decreasing energy demands of nestlings. Studies on seabirds have shown that chick energy budgets peak in the middle of the developmental period and fall as chicks approach fledging age (Simons & Whittow 1984, Cairns 1987, Coulson 2011). Kittiwake chick growth rate increases linearly until chicks are ~20 days old (Coulson & Porter 1985) after which growth rate decreases (Merkling *et al.* 2012, Vincenzi *et al.* 2013). Chicks require less food after the period of maximum growth which is reflected by a decline in energy demand (Coulson & Porter 1985, Cairns 1987). It is thought that beyond a given threshold, prey availability has no effect on feeding rate and breeding success (Burger & Piatt 1990, Phillips *et al.* 1996). Hence, when food availability is good, parents are able to adjust foraging effort to chick energy demand (Suryan *et al.* 2002), which may explain the high productivity and short trip durations observed in this study.

Seabird nest attendance has been related to temporal changes in food availability and chick demand (Gaston & Nettleship 1982, Coulson & Johnson 1993). The probability of one parent attending a nest when an adult returned with food declined as brood age increased in our study; the probability of a nest being attended was ~50% when broods were 25 days old. Previous studies have also shown Kittiwake nest attendance to decline throughout the chick-rearing period (Coulson & Johnson 1993, Cadiou & Monnat 1996) although the age at which chicks are first left alone at the nest varies among individuals (Coulson & Johnson 1993) and is dependent on annual food availability (Hamer *et al.* 1993).

Intra-brood resource allocation varied with increasing brood age. The probability of B chicks being fed first during multiple feed bouts and receiving a higher proportion of total feeds delivered to a brood increased with brood age. As timing of peak growth differs between seabird chicks in asynchronous broods (Braun & Hunt 1983, Moreno *et al.* 1994), B chicks might be expected to be smaller than A chicks prior to reaching peak mass, and therefore be less competitive. Older chicks tend to be more dominant and aggressive than younger chicks, and therefore win competitive interactions more frequently (Drummond & Osorno

1992, Merkling *et al.* 2014). However, as intra-brood variation in weight declines as seabird chicks approach fledging age (Williams & Croxall 1991), competitive abilities of younger chicks should more closely match those of their older siblings later in the developmental period. Change in intra-brood resource allocation could explain the similarities in growth rates, overall chick feeding rates and pre-fledging survival between chicks of different hatching order.

Only by considering resource allocation throughout the developmental period can we gain a more complete understanding of differential parental investment in asynchronous broods and its effect on offspring survival. We recommend that the mass and energy content of regurgitates fed to chicks in asynchronously hatching broods be examined throughout the developmental period to determine the influence of regurgitate content on parental resource allocation and chick growth rate and survival.

## ACKNOWLEDGEMENTS

Thanks go to staff and volunteers of Coquet Island RSPB Reserve, Northumberland for help during fieldwork and to Paul Morrison and Hilary Brooker-Carey for advice and logistical support. Assistance in recording hatch dates and fledging success of study nests was provided by Wesley Davies and Adam Murphy. We are grateful to Sunny Townsend and Paul Johnson for statistical advice and to Valeria Marasco for providing comments on an earlier draft. Licences to carry out work on Coquet Island were provided by Natural England and permits for ringing and marking chicks were issued by the British Trust for Ornithology. Rings were provided by Chris Redfern.

## FUNDING

This work was supported by the National Environment Research Council (award number NE/I528369/1) and the Royal Society for the Protection of Birds through a CASE studentship to the University of Glasgow.

## REFERENCES

- Abrams, P. 1991. Life history and the relationship between food availability and foraging effort. *Ecology* **72**: 1242–1252.
- Aebischer, N.J. & Coulson, J.C. 1990. Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. *J. Anim. Ecol.* **59**: 1063–1071.
- Anderson, D.J. & Ricklefs, R.E. 1992. Brood size and food provisioning in masked and Blue-footed Boobies (*Sula* spp.). *Ecology* **73**: 1363–1374.

- Bates, D., Maechler, M., Bolker, B. & Walker, S.** 2014. lme4: Linear mixed-effects models using Eigen and S4, R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>.
- Bertram, D.F., Kaiser, G.W., Ydenberg, R.C. & Url, S.** 1991. Patterns in the provisioning and growth of nestling Rhinoceros Auklets. *Auk* **108**: 842–852.
- Braun, B.M. & Hunt, G.L.** 1983. Brood reduction in Black-legged Kittiwakes. *Auk* **100**: 469–476.
- Brewer, J.H., O'Reilly, K.M. & Buck, C.L.** 2008. Effects of investigator disturbance on corticosterone concentrations of Black-legged Kittiwake chicks. *J. Field Ornithol.* **79**: 391–398.
- Burger, A.E. & Piatt, J.F.** 1990. Flexible time budgets in breeding Common Murres: buffers against variable prey abundance. *Stud. Avian Biol.* **14**: 71–83.
- Cadiou, B. & Monnat, J.Y.** 1996. Parental attendance and squatting in the kittiwake *Rissa tridactyla* during the rearing period. *Bird Study* **43**: 164–171.
- Cairns, D.K.** 1987. The ecology and energetics of chick provisioning by Black Guillemots. *Condor* **89**: 627–635.
- Cairns, D.K.** 1988. Seabirds as indicators of marine food supplies. *Biol. Oceanogr.* **5**: 261–271.
- Chiaradia, A.F. & Kerry, K.R.** 1999. Daily nest attendance and breeding performance in the Little Penguin *Eudyptula minor* at Phillip Island, Australia. *Mar. Ornithol.* **27**: 13–20.
- Clark, A.B. & Wilson, D.S.** 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Q. Rev. Biol.* **56**: 253–277.
- Cook, M.I., Monaghan, P. & Burns, M.D.** 2000. Effects of short-term hunger and competitive asymmetry on facultative aggression in nestling Black Guillemots *Cepphus grylle*. *Behav. Ecol.* **11**: 282–287.
- Coulson, J.C.** 2011. *The Kittiwake*. T & A D Poyser, London.
- Coulson, J.C. & Coulson, B.A.** 2008. Measuring immigration and philopatry in seabirds; recruitment to Black-legged Kittiwake colonies. *Ibis* **150**: 288–299.
- Coulson, J.C. & Johnson, M.P.** 1993. The attendance and absence of adult kittiwakes *Rissa tridactyla* from the nest site during the chick stage. *Ibis* **135**: 372–378.
- Coulson, J.C. & Porter, J.M.** 1985. Reproductive success of the kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis* **127**: 450–466.
- Coulson, J.C. & Thomas, C.S.** 1985. Changes in the biology of the kittiwake *Rissa tridactyla*: a 31-year study of a breeding colony. *J. Anim. Ecol.* **54**: 9–26.
- Coulson, J.C. & White, E.** 1961. An analysis of the factors influencing the clutch size of the kittiwake. *Proc. Zool. Soc. Lond.* **136**: 207–217.
- Crawley, M.J.** 2007. *The R Book*. John Wiley & Sons Ltd, Chichester.
- Croxall, J.P., Reid, K. & Prince, P.A.** 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar. Ecol. Prog. Ser.* **177**: 115–131.
- Davies, L.S. & McCaffrey, F.T.** 1986. Survival analysis of eggs and chicks of Adélie penguins (*Pygoscelis adeliae*). *Auk* **103**: 379–388.
- Donazar, J.A. & Ceballos, O.** 1989. Growth rates of nestling Egyptian vultures *Neophron percnopterus* in relation to brood size, hatching order and environmental factors. *Ardea* **77**: 217–226.
- Drent, R.H. & Daan, S.** 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**: 225–252.
- Drummond, H.** 2002. Begging versus aggression in avian broodmate competition. In Wright, J. & Leonard, M.L. (eds) *The Evolution of Begging*, 337–360. Kluwer Academic Publishers, Dordrecht.
- Drummond, H. & Osorno, J.L.** 1992. Training siblings to be submissive losers: dominance between booby nestlings. *Anim. Behav.* **44**: 881–893.
- Emms, S.K. & Verbeek, N.A.** 1991. Brood size, food provisioning and chick growth in the Pigeon Guillemot *Cepphus columba*. *Condor* **93**: 943–951.
- Erikstad, K.E., Fauchald, P., Tveraa, T. & Steen, H.** 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* **79**: 1781–1788.
- Fielding, A.H. & Bell, J.F.** 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* **24**: 38–49.
- Frederiksen, M., Edwards, M., Mavor, R.A. & Wanless, S.** 2007. Regional and annual variation in Black-legged Kittiwake breeding productivity is related to sea surface temperature. *Mar. Ecol. Prog. Ser.* **350**: 137–143.
- Galbraith, H.** 1983. The diet and feeding ecology of breeding kittiwakes *Rissa tridactyla*. *Bird Study* **30**: 109–120.
- Gaston, A.J. & Nettleship, D.N.** 1982. Factors determining seasonal changes in attendance at colonies of the Thick-billed Murre *Uria lomvia*. *Auk* **99**: 468–473.
- Gill, V.A., Hatch, S.A. & Lanctot, R.B.** 2002. Sensitivity of breeding parameters to food supply in Black-legged kittiwakes *Rissa tridactyla*. *Ibis* **144**: 268–283.
- Godfray, H.C.J.** 1995. Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. *Am. Nat.* **146**: 1–24.
- Golet, G.H., Kuletz, K.J., Roby, D.D., Irons, D.B., Olet, G.H.G., Uletz, K.J.K. & Oby, D.D.R.** 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. *Auk* **117**: 82–91.
- Granadeiro, J.P., Bolton, M., Silva, M.C., Nunes, M. & Furness, R.W.** 2000. Responses of breeding Cory's Shearwater *Calonectris diomedea* to experimental manipulation of chick condition. *Behav. Ecol.* **11**: 274–281.
- Hahn, D.C.** 1981. Asynchronous hatching in the Laughing Gull: cutting losses and reducing rivalry. *Anim. Behav.* **29**: 421–427.
- Hamer, K.C., Monaghan, P., Uttley, J.D., Walton, P. & Burns, M.D.** 1993. The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. *Ibis* **135**: 255–263.
- Hillström, L., Kilpi, M. & Lindström, K.** 2000. Is asynchronous hatching adaptive in Herring Gulls (*Larus argentatus*)? *Behav. Ecol. Sociobiol.* **47**: 304–311.
- Jacobsen, K-O., Erikstad, K.E. & Sæther, B-E.** 1995. An experimental study of the costs of reproduction in the kittiwake *Rissa tridactyla*. *Ecology* **76**: 1636–1642.
- Jodice, P.G.R., Roby, D.D., Hatch, S.A., Gill, V.A., Lanctot, R.B. & Visser, G.H.** 2002. Does food availability affect energy expenditure rates of nesting seabirds? A supplemental-feeding experiment with Black-legged Kittiwakes (*Rissa tridactyla*). *Can. J. Zool.* **80**: 214–222.
- Kersten, M. & Brenninkmeijer, A.** 1995. Growth, fledging success and post-fledging survival of juvenile oystercatchers *Haematopus ostralegus*. *Ibis* **137**: 396–404.
- Kloskowski, J.** 2001. Temporal patterns of parental resource distribution in the red-necked grebe: equalizing the share of the survivors. *Behaviour* **138**: 1355–1370.
- Lack, D.** 1947. The significance of clutch size. Parts I and II. *Ibis* **89**: 302–352.
- Lack, D.** 1954. *The Natural Regulation of Animal Numbers*. Oxford University Press, London.
- Lewis, S., Wanless, S., Wright, P.J., Harris, M.P., Bull, J. & Elston, D.A.** 2001. Diet and breeding performance of Black-legged Kittiwakes *Rissa tridactyla* at a North sea colony. *Mar. Ecol. Prog. Ser.* **221**: 277–284.
- Lewis, S., Hamer, K.C., Money, L., Griffiths, R., Wanless, S. & Sherratt, T.N.** 2004. Brood neglect and contingent foraging behavior in a pelagic seabird. *Behav. Ecol. Sociobiol.* **56**: 81–88.

- Low, M., Makan, T. & Castro, I.** 2012. Food availability and offspring demand influence sex-specific patterns and repeatability of parental provisioning. *Behav. Ecol.* **23**: 25–34.
- Magrath, R.D.** 1990. Hatching asynchrony in altricial birds. *Biol. Rev.* **65**: 587–622.
- Maunder, J.E. & Threlfall, W.** 1972. The breeding biology of the Black-legged Kittiwake in Newfoundland. *Auk* **89**: 789–816.
- Merkling, T., Leclaire, S., Danchin, E., Lhuillier, E., Wagner, R.H., White, J., Hatch, S.A. & Blanchard, P.** 2012. Food availability and offspring sex in a monogamous seabird: insights from an experimental approach. *Behav. Ecol.* **23**: 751–758.
- Merkling, T., Agdere, L., Albert, E., Durieux, R., Hatch, S.A., Danchin, E. & Blanchard, P.** 2014. Is natural hatching asynchrony optimal? An experimental investigation of sibling competition patterns in a facultatively siblicidal seabird. *Behav. Ecol. Sociobiol.* **68**: 309–319.
- Mock, D.W. & Schwagmeyer, P.L.** 1990. The peak load reduction hypothesis for avian hatching asynchrony. *Evol. Ecol.* **4**: 249–260.
- Monaghan, P., Walton, P., Wanless, S., Uttley, J.D. & Burns, M.D.** 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. *Ibis* **136**: 214–222.
- Moreno, J., Carrascal, L.M., Sanz, J.J., Amat, J.A. & Cuervo, J.J.** 1994. Hatching asynchrony, sibling hierarchies and brood reduction in the Chinstrap Penguin *Pygoscelis antarctica*. *Polar Biol.* **14**: 21–30.
- Murphy, E.C., Springer, A.M. & Roseneau, D.G.** 1991. High annual variability in reproductive success of kittiwakes (*Rissa tridactyla* L.) at a colony in Western Alaska. *J. Anim. Ecol.* **60**: 515–534.
- Nisbet, I.C.T., Spendelov, J.A. & Hatfield, J.S.** 1995. Variations in growth of roseate tern chicks. *Condor* **97**: 335–344.
- O'Connor, R.J.** 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? *Anim. Behav.* **26**: 79–96.
- Parker, G.A., Royle, N.J. & Hartley, I.R.** 2002. Intrafamilial conflict and parental investment: a synthesis. *Proc. R. Soc. B* **357**: 295–307.
- Pearce, J. & Ferrier, S.** 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Modell.* **133**: 225–245.
- Petersen, S.L., Ryan, P.G. & Grémillet, D.** 2006. Is food availability limiting in African Penguins *Spheniscus demersus* at boulders? A comparison of foraging effort at mainland and island colonies. *Ibis* **148**: 14–26.
- Phillips, R.A., Caldow, R.W.G. & Furness, R.W.** 1996. The influence of food availability on the breeding effort and reproductive success of Arctic Skuas *Stercorarius parasiticus*. *Ibis* **138**: 410–419.
- Price, K. & Ydenberg, R.** 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. *Behav. Ecol. Sociobiol.* **37**: 201–208.
- Price, K., Harvey, H. & Ydenberg, R.** 1996. Begging tactics of nestling Yellow-headed Blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Anim. Behav.* **51**: 421–435.
- Pugesek, B.H.** 1990. Parental effort in the California Gull: tests of parent-offspring conflict theory. *Behav. Ecol. Sociobiol.* **27**: 211–215.
- R Core Development Team.** 2014. *R: A Language and Environment for Statistical Computing v. 3.1.2*. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/> [accessed 10 February 2014].
- Redondo, T. & Carranza, J.** 1989. Offspring reproductive value and nest defense in the magpie (*Pica pica*). *Behav. Ecol. Sociobiol.* **25**: 369–378.
- Ricklefs, R.E.** 1965. Brood reduction in the curve-billed thrasher. *Condor* **67**: 505–510.
- Ricklefs, R.E.** 1987. Response of adult Leach's Storm-petrels to increased food demand at the nest. *Auk* **104**: 750–756.
- Ricklefs, R.E. & White, S.C.** 1981. Growth and energetics of chicks of the Sooty Tern (*Sterna fuscata*) and common tern (*S. hirundo*). *Auk* **98**: 361–378.
- Ricklefs, R.E., Day, C.H., Huntington, C.E. & Williams, J.B.** 1985. Variability in feeding rate and meal size of Leach's Storm-petrel at Kent Island, New Brunswick. *J. Anim. Ecol.* **54**: 883–898.
- Robertson, G.S., Bolton, M., Grecian, W.J. & Monaghan, P.** 2014. Inter- and intra-year variation in foraging areas of breeding kittiwakes (*Rissa tridactyla*). *Mar. Biol.* **161**: 1973–1986.
- Roby, D.D.** 1991. Diet and postnatal energetics in convergent taxa of plankton-feeding seabirds. *Auk* **108**: 131–146.
- Rogowitz, G.L.** 1996. Trade-offs in energy allocation during lactation. *Am. Zool.* **36**: 197–204.
- Rogowitz, G.L. & McClure, P.A.** 1995. Energy export and offspring growth during lactation in cotton rats (*Sigmodon hispidus*). *Func. Ecol.* **9**: 143–150.
- Royle, N.J., Hartley, I.R. & Parker, G.A.** 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends Ecol. Evol.* **17**: 434–440.
- Royle, N.J., Hartley, I.R. & Parker, G.A.** 2004. Parental investment and family dynamics: interactions between theory and empirical tests. *Popul. Ecol.* **46**: 231–241.
- Royle, N.J., Smiseth, P.T. & Kölliker, M.** 2012. *The Evolution of Parental Care*. Oxford University Press, Oxford.
- Sandvik, H. & Barrett, R.T.** 2001. Effect of investigator disturbance on the breeding success of the Black-legged Kittiwake. *J. Field Ornithol.* **72**: 30–42.
- Sargent, R.C. & Gross, M.R.** 1986. William's principle: an explanation of parental care in teleost fishes. In Pitcher, T.J. (ed.) *The Behavior of Teleost Fishes*, 275–293. Croom Helm, London.
- Seddon, P.J. & van Heezik, Y.** 1991. Effects of hatching order, sibling asymmetries, and nest site on survival analysis of Jackass Penguin chicks. *Auk* **108**: 548–555.
- Shizuka, D. & Lyon, B.E.** 2009. Family dynamics through time: brood reduction followed by parental compensation with aggression and favouritism. *Ecol. Lett.* **16**: 315–322.
- Simons, T.R. & Whittow, G.C.** 1984. Energetics of breeding Dark-rumped Petrels. In Whittow, G.C. & Rahn, H. (eds) *Seabird Energetic*, 159–181. Springer, New York.
- Skórka, P., Wójcik, J.D., Martyka, R. & Lenda, M.** 2012. Numerical and behavioural response of Black-headed Gulls *Chroicocephalus ridibundus* on population growth of the expansive Caspian Gull *Larus cachinnans*. *J. Ornithol.* **153**: 947–961.
- Spahn, S.A. & Sherry, T.W.** 1999. Cadmium and lead exposure associated with reduced growth rates, poorer fledging success of Little Blue Heron Chicks (*Egretta caerulea*) in South Louisiana wetlands. *Arch. Environ. Con. Tox.* **37**: 377–384.
- Stenning, M.J.** 1996. Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. *Trends Ecol. Evol.* **11**: 243–246.
- Stienen, E.W.M. & Brenninkmeijer, A.** 2006. Effect of brood size and hatching sequence on pre-fledging mortality of Sandwich Terns: why lay two eggs? *J. Ornithol.* **147**: 520–530.
- Suryan, R.M., Irons, D.B., Kaufman, M., Benson, J., Jodice, P.G.R., Roby, D.D. & Brown, E.D.** 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the Black-legged Kittiwake *Rissa tridactyla*. *Mar. Ecol. Prog. Ser.* **236**: 273–287.
- Tveraa, T., Sether, B.E., Aanes, R. & Erikstad, K.E.** 1998. Regulation of food provisioning in the Antarctic petrel; the importance of parental body condition and chick body mass. *J. Anim. Ecol.* **67**: 699–704.
- Vincenzi, S., Hatch, S., Mangel, M. & Kitaysky, A.** 2013. Food availability affects onset of reproduction in a long-lived seabird. *Proc. R. Soc. B.* doi:10.1098/rspb.2013.0554.

**White, J., Leclaire, S., Kriloff, M., Mulard, H., Hatch, S.A. & Danchin, E.** 2010. Sustained increase in food supplies reduces broodmate aggression in Black-legged Kittiwakes. *Anim. Behav.* **79**: 1095–1100.

**Williams, T.D. & Croxall, J.P.** 1991. Chick growth and survival in Gentoo Penguins (*Pygoscelis papua*): effect of hatching asynchrony and variation in food supply. *Polar Biol.* **11**: 197–202.

(MS received 4 November 2014; revised MS accepted 2 April 2015)