Is natural hatching asynchrony optimal? An experimental investigation of sibling competition patterns in a facultatively siblicidal seabird

Thomas Merkling, Lena Agdere, Elise Albert, Romain Durieux, Scott A. Hatch, Etienne Danchin & Pierrick Blanchard
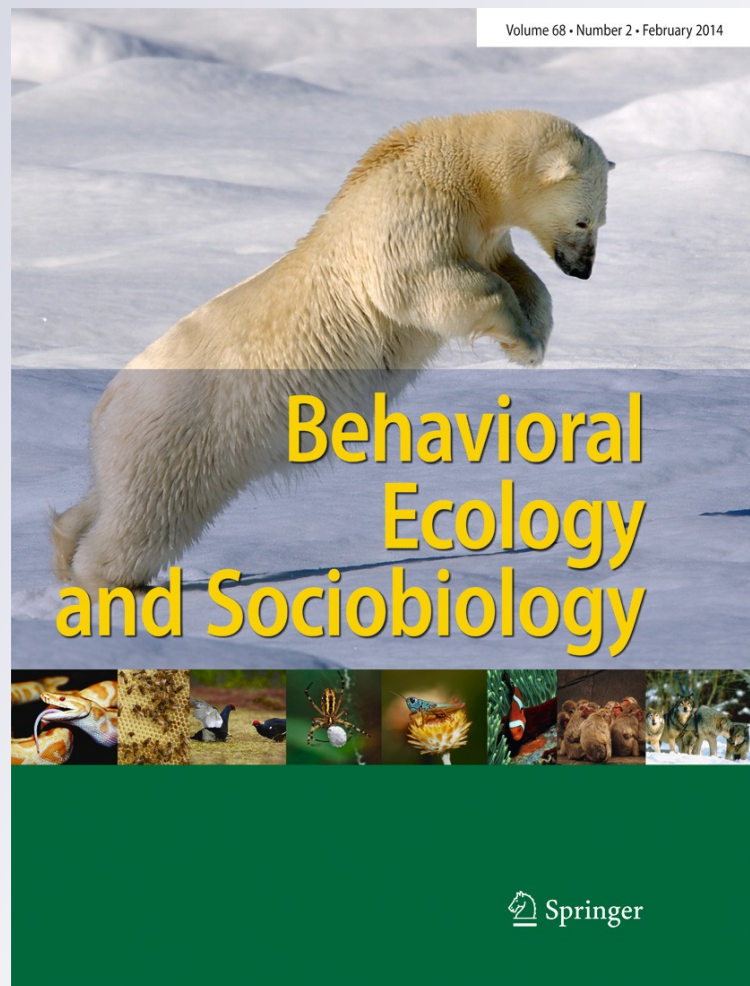
Volume 68 · Number 2 · February 2014

Behavioral Ecology and Sociobiology

🐎 Springer

🐎 Springer

Springer

ORIGINAL PAPER

Is natural hatching asynchrony optimal? An experimental investigation of sibling competition patterns in a facultatively siblicidal seabird

**Thomas Merkling · Lena Agdere · Elise Albert ·
Romain Durieux · Scott A. Hatch · Etienne Danchin ·
Pierrick Blanchard**

Abstract In unpredictable environments, any tactic that enables avian parents to adjust brood size and, thus, energy expenditure to environmental conditions should be favoured. Hatching asynchrony (HA), which occurs whenever incubation commences before clutch completion, may comprise such a tactic. For instance, the sibling rivalry hypothesis states that the hierarchy among chicks, concomitant to HA, should both facilitate the adjustment of brood size to environmental conditions and reduce several components of sibling competition as compared to synchronous hatching, at both brood and individual levels. We thus predicted that brood aggression, begging and feeding rates should decrease and that older chick superiority should increase with HA increasing, leading to higher growth and survival rates. Accordingly, we investigated the effects of an experimental upward and downward manipulation of HA magnitude on behaviour, growth and survival of black-legged kittiwake (*Rissa tridactyla*) chicks. In line with the sibling rivalry hypothesis, synchronous hatching increased aggression and tended to increase feeding rates by parents at the brood level. Begging rates, however, increased with HA contrary to our expectations. At the individual level, as HA magnitude increased, the younger chick was attacked and begged proportionally more often, experienced a slower growth and a higher mortality than its sibling. Overall, the occurrence of energetic costs triggered by synchronous hatching both for parents and chicks, together with the lower growth rate and increased mortality of the younger chick in highly asynchronous broods suggest that natural HA magnitude may be optimal.

Keywords Aggression · Begging · Hatching asynchrony · Kittiwake · Sibling competition · Sibling rivalry hypothesis

T. Merkling (✉) · L. Agdere · E. Albert · R. Durieux · E. Danchin ·
P. Blanchard
UMR5174 EDB (Laboratoire Évolution & Diversité Biologique),
CNRS, ENFA, Université Toulouse 3 Paul Sabatier,
118 Route de Narbonne,, 31062 Toulouse, France
e-mail: thomasmerkling00@gmail.com

T. Merkling · L. Agdere · E. Albert · R. Durieux · E. Danchin ·
P. Blanchard
CNRS, UMR5174 EDB, Université Paul Sabatier,
31062 Toulouse, France

S. A. Hatch
U.S. Geological Survey, Alaska Science Center,
4210 University Drive, Anchorage, AK 99508, USA

Present Address:
S. A. Hatch
Institute for Seabird Research and Conservation,
12850 Mountain Place, Anchorage, AK 99516, USA

Introduction

In unpredictable environments, female birds often lay more eggs than the number of chicks the pair would be able to fledge under average environmental conditions (Lack 1954; Ricklefs 1965). This strategy allows pairs to produce more chicks than average when environmental conditions turn out to be good. These occasional fitness gains are supposed to exceed costs of caring for extra chicks doomed to die under average or poor environmental conditions (the facultative brood reduction hypothesis, Lack 1947, 1954). Hence, any tactic favouring the facultative elimination of the weakest chick(s) at low costs according to environmental conditions should be advantageous for parents.

Hatching asynchrony (HA) is common among birds. It occurs whenever incubation commences before the clutch completion and may have evolved, for instance, in response

to the threat of nest predation (Hussell 1972; reviewed in Stenning 1996). However, other hypotheses have focused on its importance as a reproductive tactic per se (reviewed in Magrath 1990; Stenning 1996), by emphasising that size differences among nestlings arising from HA allow parents to adjust food allocation and thus chicks' fate according to environmental conditions. Among these hypotheses, the sibling rivalry hypothesis (Hahn 1981) states that the natural hierarchy establishment, concomitant to HA, should minimise sibling competition, thereby reducing energy wastage (Hamilton 1964) and allow parents to preferentially feed the older chick when needed. Accordingly, variation in HA magnitude should impact parental fitness through its consequences on chick behaviour at both brood and individual levels.

At the brood level, natural HA is thought to reduce the potential for escalated conflict among hatchlings, whereas synchronous hatching would minimise size differences and lead to wasted energy among chicks through increased aggression and begging rates, in accordance with game theory models (Maynard-Smith 1982). As parents typically feed their chicks below their maximum capacity (e.g. Mock and Ploger 1987; Gilby et al. 2011), they may be able to increase their feeding effort in response to an unexpected increase in brood demand (as predicted in synchronous broods) (Ostreiher et al. 2012), as long as it does not jeopardise their subsequent survival and reproduction (Williams 1966; Drent and Daan 1980; Stearns 1992). The increased feeding effort may, however, not be sufficient to overcome energy wastage in synchronous broods (Gilby et al. 2011). Consequently, the average chick growth and survival in synchronous broods should be lower than those in asynchronous broods, for a given set of environmental conditions (Hahn 1981).

At the individual level, as HA leads to an early disparity in chick fighting abilities, a dominance hierarchy develops among siblings. Hence, theoretically, the higher the magnitude of HA, the more the smaller chicks should be submissive (Maynard-Smith and Parker 1976). When environmental conditions are too poor for parents to fledge all chicks, they are expected to preferentially feed older sibs, with smaller/younger sibs eventually dying from starvation and stress (Lack 1947), thereby shortening period of energetic wastage for parents. Under good environmental conditions, however, food would be sufficient for smaller/younger sibs to fledge as well. Thus, HA could be advantageous for parents in all environmental conditions.

Several studies have provided experimental evidence for the sibling rivalry hypothesis (Hahn 1981) both in species where chicks compete via begging (i.e. 'sublethal sibling competition') or via overt aggressions (i.e. 'lethal sibling competition', Roulin and Dreiss 2012). In particular, aggression and/or begging rates were found to be higher in experimentally synchronous broods than in naturally asynchronous broods (Fujioka 1985; Mock and Ploger 1987; Osorno and

Drummond 1995; Viñuela 1999; Gilby et al. 2011). When HA was experimentally increased as compared to natural asynchronous conditions, begging rate further decreased (Mock and Ploger 1987). At first sight, the same pattern could have been expected for aggression rate as older sibs could display less aggressive behaviours to establish their dominance in highly asynchronous broods (Forbes 1991). Surprisingly, most studies reported that brood aggression rate was higher for experimentally increased HA than for controls, leading to a U-shaped curve between aggression rate and HA, with a minimum intensity for natural values of HA (Osorno and Drummond 1995; Viñuela 1999). Furthermore, contrary to predictions, parents responded to a synchronous brood's higher demand by feeding their chicks more often, which, nevertheless, conferred no growth advantage (Fujioka 1985; Mock and Ploger 1987; Gilby et al. 2011). At the individual level, as the magnitude of the experimental HA increased, the eldest chick became proportionally more aggressive, begged more and was fed more often than its sibling(s) (Mock and Ploger 1987; Osorno and Drummond 1995; Gilby et al. 2011). However, results relating HA magnitude to chick growth and survival are quite inconsistent (e.g. Fujioka 1985; Royle and Hamer 1998; Viñuela 2000; Gilby et al. 2011; Podlas and Richner 2013), except that subordinate chicks suffer higher mortality in broods with HA magnitude higher than natural (Osorno and Drummond 1995; Viñuela 2000). As sibling competition entails two possible modes of energy wastage, begging and overt aggressions, species exhibiting both might be particularly suitable to test the sibling rivalry hypothesis (Hahn 1981). Yet, no study investigated the influence of upward and downward manipulation of HA on chick and parental behaviour, both at the brood and individual levels, along with its consequences on chick growth and survival.

Here we performed such a study in the black-legged kittiwake, Rissa tridactyla, a facultatively siblicidal seabird (Braun and Hunt 1983). Females usually lay two eggs hatching asynchronously (mean, 1.35 days in our study population, Gill et al. 2002). The first-hatched chick (A chick) becomes dominant over the second one (B chick) in few hours via overt aggression, and the latter responds submissively ('aggression–submission dominance relationship', Drummond 2006; see also Braun and Hunt 1983). Aggression is related to food availability (Irons 1992; White et al. 2010) and female feeding effort (Leclaire et al. 2010). Moreover, in natural conditions, A chicks beg more and are fed more often than B chicks (Braun and Hunt 1983; White et al. 2010), promoting faster growth (Merkling et al. 2012). We experimentally manipulated HA magnitude from 0 to 3 days. We then recorded chick behaviour (aggression, begging and probability of being fed) and monitored chick growth and survival. Following the sibling rivalry hypothesis (Hahn 1981) and pertinent experimental studies, we predicted that, at the brood level, begging and feeding frequencies would decrease with increasing HA (from

0 to 3 days), while the relationship would be quadratic for aggression, with minimal frequencies for intermediate values of HA (i.e. close to natural conditions), as found in previous studies (e.g. Osorno and Drummond 1995). At the individual level, we predicted that A chick superiority in terms of aggression, begging, feeding probability and growth would increase with HA magnitude. Finally, we expected A chicks to have a lower survival rate in synchronous broods than in more asynchronous broods, whereas B chicks would suffer higher mortality in highly asynchronous broods than in synchronous or naturally asynchronous broods.

Materials and methods

Study site

The study was carried out from mid-May to mid-August 2011 in a population of black-legged kittiwakes nesting on an abandoned U.S. Air Force radar tower on Middleton Island (59° 26′N, 146° 20′W), Gulf of Alaska. The tower is a 12-walled polygon where artificial nest sites have been created on the upper walls. Observations (from a distance of 20 cm) from inside the building through one-way window glass allow us to easily monitor the breeders and their chicks (for details, see Gill and Hatch 2002). Besides behavioural monitoring (see 'Behavioural observations' below), nests were checked twice daily (0900 and 1800 hours) throughout the breeding season to record events such as laying, hatching and chick mortality.

Experimental design

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

Hatching occurred in the incubator, and its timing was assessed to the nearest 2 h between 0600 and 2200 hours and to the nearest 6 h at night. We then weighed each chick to the nearest 0.1 g with an electronic scale, measured head-bill and tarsus lengths to the nearest 0.1 mm with a calliper and measured wing length to the nearest 1 mm with a wing ruler. Chicks were marked on the head with a nontoxic marker to identify their original rank.

To control for parental effects, we then put each chick in a foster nest to create experimental broods of two unrelated chicks, an A chick and a B chick. By choosing chicks according to their hatching date, we experimentally set the magnitude of HA (defined as B chick hatching date minus A chick hatching date) from synchronous (i.e. 0-day interval) to highly asynchronous broods (i.e. 3-day interval) (mean ± standard error (SE), 1.3±0.09 days, $N=107$), with the A chick having hatched before or at the same time as the B chick in all but one nest. The mean natural hatching interval (for pairs that had their two eggs hatched in the incubator) was 1.64 days (SE± 0.07 days, $N=117$), which is slightly higher than previously reported in the same colony, mean ± SE 1.35±0.09 days (Gill et al. 2002). Our experimental manipulation thus encompassed the mean natural hatching interval and entailed a wide, but biologically plausible, range around it.

Behavioural observations

We arbitrarily assigned a number to each nest and randomised the order of observations. Instantaneous scan sampling (Altmann 1974) was performed for each nest three times a day (at 1000, 1400 and 1800 hours). For each chick, we recorded whether it was begging (i.e. pecking its parent's bill), being aggressive toward its sibling (i.e. pecking any part of its sibling's body), being fed or exhibited none of those three behaviours. Nests were observed from the day the B chick was put in the nest until it was 20 days old (i.e. the period when most aggressiveness occur, White et al. 2010; Leclaire et al. 2011) or until one of the chicks died. A total of 8,618 observations were performed on 107 nests.

Measuring chick growth

Chicks were measured every 5 days from day 5 to day 35. Although fledging usually occurs at an older age (after 40 days, Hatch et al. 2009), we did not handle chicks after 35 days old to avoid premature fledging. The same measurements were taken as those described for the hatching stage (see 'Experimental design' above).

We ran a principal component analysis on wing, tarsus and head-bill lengths on all ages. We then considered the score of each individual on the first principal component (94 % of total variance explained) as a measure of its structural size at a given age (e.g. Blanchard et al. 2007). We calculated the mass gain and the structural size growth rate between 0 and 10 days (instead of between 0 and 20 days in order to maximise sample size), by estimating the slope of the linear regression between body mass and age and between structural size and age, respectively. We also considered maximal body mass and structural size for chicks that survived until at least 30 days.

Data analyses

For each analysis (behaviour, growth and survival), we started with a complete statistical model and successively removed terms beginning with those of the highest degree. We compared the change in deviance after removal of a term, using a χ^2 test with the appropriate degrees of freedom (likelihood ratio test). When an interaction was tested, the corresponding main effects were kept in the model. All analyses were conducted with R 2.14.2 (R Development Core Team 2012). Mean values (±SE) are shown.

Behavioural observations

To investigate whether the patterns observed were true overall or specific to a period, we analysed behavioural observations using the whole observation period and by sub-periods containing the first 10 days or the last 10 days.

At the brood level, we looked at the effect of HA on behaviour using generalised linear mixed models (GLMMs) with a binomial error distribution and a logit link function as the response variable was binary (i.e. absence or presence of one of the studied behaviours). We used a maximum likelihood estimator (*lme4* package, Bates et al. 2011) with nest and individual (nested within nest) included as random effects to account for the non-independence of observations from the same nest and from the same individual within a nest. Based on our predictions, we were only interested in the quadratic and the linear models. Hence, for each behaviour and period, we first considered the quadratic model containing HA, HA^2 and chick age and B chick hatching date (i.e. to correct for a potential seasonal effect) as covariates (reported only when significant). When HA^2 was significant, we kept HA regardless of its significance. Otherwise, we removed HA^2 from the complete model for further comparisons.

Behaviour were then analysed at the individual level. We wanted to consider the interactions between all explanatory variables and chick rank, but it led to GLMM convergence problems due to the small occurrence of aggression and feeding behaviours. To circumvent them, we used the rate at which A chick displayed each behaviour as a response variable (e.g. 1=the A chick was the only one seen exhibiting a given behaviour; 0=B chick only) in a GLM (aggression, $N=26$ nests; begging, $N=62$; feeding, $N=29$). This led to more simple models without interactions or random terms. The complete quadratic model contained HA^2, HA and B chick hatching date as a covariate (reported only when significant).

Chick growth

For the four chick growth parameters we considered as dependent variables, the complete linear mixed model contained the interactions between rank and HA^2 and between rank and HA.

It also contained B chick hatching date as a covariate (reported only when significant) and nest as a random effect. To meet model assumptions (normality and homoscedasticity of data and residuals), we used the Box–Cox transformation (Box and Cox 1964) in the *MASS* package (Venables and Ripley 2002) on mass gain ($\lambda=1.7$) and structural size growth rate ($\lambda=2.4$) (A chicks, $N=98$; B chicks, $N=83$) as well as on maximal body mass ($\lambda=2.5$) and maximal structural size ($\lambda=4.9$) (A chicks, $N=83$; B chicks, $N=58$). Due to chick mortality, sample sizes were larger for analyses of mass gain and structural size growth rate than for analyses of maximal values.

Chick survival

Birth date was known for every chick, but death date was not known for chicks that were still alive when we left the field. Hence, we used either fledging age ($N=87$) or age at our departure from the field for unfledged individuals ($N=50$) as the age of last sighting of the individuals. Age for unfledged individuals still alive when we left ranged between 34 and 50 days. Because survival at this age is very high (Fig. 5, see also Barrett and Runde 1980), we are confident that those chicks fledged after our departure and could therefore be considered as survivors. As survival was not independent for chicks in the same nest, we used Cox proportional hazards mixed regression models (CPH mixed) in the *coxme* package (Therneau 2012), with nest included as a random effect when considering both ranks (A chicks, $N=104$; B chicks, $N=102$). We tested the only interaction between rank and HA.

Results

Influence of HA on aggression, begging and feeding at the brood level

Before 10 days, the quadratic relationship between aggression frequency and HA was significant (Table 1), with synchronous and highly asynchronous broods having a higher aggression frequency than broods with a medium HA magnitude (Fig. 1). No significant relationship between aggression frequency and HA or HA^2 was found after 10 days, while in the entire set of observations, the negative linear relationship between aggression frequency and HA was marginally significant (Table 1). Aggression frequency decreased with chick age both overall and before 10 days (Table 1). It also decreased with hatching date, but only after 10 days (Table 1).

Begging frequency increased linearly, although not significantly, with HA before 10 days, but not overall or after 10 days (Table 1). It also increased with chick age both overall and before 10 days (Table 1).

Feeding frequency decreased, although not significantly, with HA overall and after 10 days, but not before 10 days

Table 1 Generalised linear mixed model selection to explain variation in aggression, begging and feeding rates at the brood level according to hatching asynchrony (HA), HA^2, hatching date and chick age for the three different time periods

Variable removed from the complete model	Before 10 days			After 10 days			Overall		
	χ^2	df	p	χ^2	df	p	χ^2	df	p
Aggression									
HA^2	**3.62**	**1**	**0.05**	0.11	1	0.74	2.59	1	0.11
HA	2.16	1	0.14[a]	1.59	1	0.21	*3.28*	*1*	*0.07*
Hatching date	0.14	1	0.71	0.99	1	0.32	0.08	1	0.78
Age	**3.98**	**1**	**0.046**	1.40	1	0.24	**28.26**	**1**	**<0.0001**
	β	SE					β	SE	
Selected model	(Intercept)	−5.09	0.54				(Intercept)	−6.52	0.30
	HA^2	0.48	0.28				Age	−0.98	0.23
	HA	−1.57	0.76[a]						
	Age	−0.71	0.37						
Begging									
HA^2	0.04	1	0.85	0.38	1	0.54	0.03	1	0.85
HA	*3.12*	*1*	*0.08*	1.58	1	0.21	0.08	1	0.77
Hatching date	0.02	1	0.87	0.35	1	0.56	0.62	1	0.43
Age	**8.70**	**1**	**0.003**	2.13	1	0.14	**14.33**	**1**	**0.0001**
	β	SE					β	SE	
Selected model	(Intercept)	−3.11	0.19				(Intercept)	−3.37	0.07
	Age	0.56	0.20				Age	0.23	0.06
Feeding									
HA^2	0.23	1	0.63	0.08	1	0.78	0.73	1	0.39
HA	0.23	1	0.63	*3.06*	*1*	*0.08*	*3.42*	*1*	*0.06*
Hatching date	**5.04**	**1**	**0.02**	0.64	1	0.42	**4.07**	**1**	**0.04**
Age	**14.18**	**1**	**0.0002**	0.22	1	0.64	**18.90**	**1**	**<0.0001**
	β	SE					β	SE	
Selected model	(Intercept)	−6.38	0.52				(Intercept)	8.6	8.4
	Hatching date	−0.49	0.23				Hatching date	−0.08	0.05
	Age	−1.45	0.41				Age	−0.72	0.19

Significant terms are highlighted in bold, while marginally significant terms are highlighted in italic (but not retained in the selected model)

χ^2 chi-square value (change in deviance), *df* difference in degrees of freedom between the two models compared, *p* p value, β estimated coefficient, *SE* standard error of the estimated coefficient

[a] When HA^2 was significant, HA was retained in the model even if not significant

(Table 1). It also decreased with chick age and hatching date both overall and before 10 days (Table 1).

Influence of HA on aggression, begging and feeding at the individual level

A chick aggression rate increased with HA overall as well as before 10 days, but not after 10 days (Table 2). B chicks were more aggressive than A chicks for HA magnitude smaller than 0.5 days, while A chicks were clearly more aggressive when HA magnitude exceeded 1 day (Fig. 2). A chick aggression rate increased, although not significantly, with hatching date before 10 days (Table 2).

A chick begging rate tended to have a quadratic relationship with HA before 10 days (Table 2, Fig. 3). A chicks begged more than their siblings for HA magnitude between approximately 0.5 and 1.8 days, while B chicks begged more when HA exceeded approximately 2.2 days (Fig. 3). No other significant effects were found overall or after 10 days (Table 2).

No significant terms were found concerning A chick feeding rate (Table 2).

Chick growth

HA significantly influenced structural size growth rate in relation to rank; it decreased linearly with HA for B chicks,
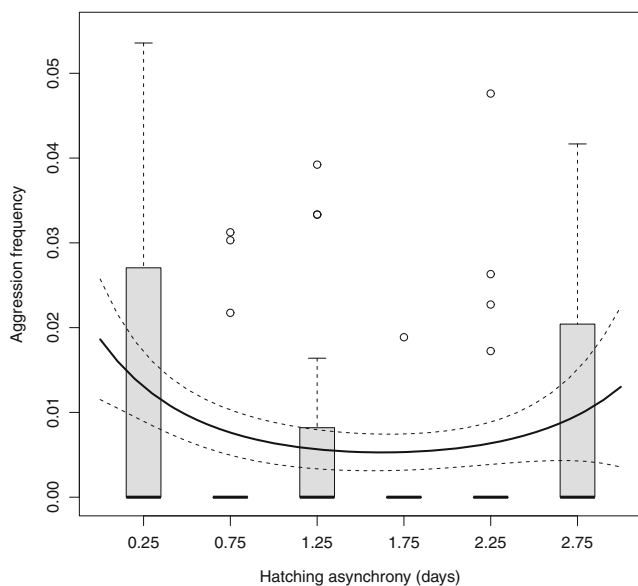
Fig. 1 The relationship between aggression frequency at the brood level and hatching asynchrony during the 10 first days after B chick hatching. Frequencies were obtained from 8,618 scan samplings on 107 nests. We grouped the data by class of 0.5 days of HA (i.e. six classes) for illustrative purposes. Observed data are represented per class by a *grey box plot* and *outliers above*, but one outlier at 0.07 in the fourth class is not shown to reduce the scale of the figure. *Solid and dashed lines* are GLMM predicted values and SE, respectively, with chick age (i.e. a significant covariate) set at 2 days. Nest and individual within nest were included as random terms in the model

but not for A chicks (LMM; interaction HA × rank, $\chi^2_1 = 8.61$, $p = 0.003$, Fig. 4). For mass gain, however, only chick rank was significant, with A chicks gaining significantly more mass than B chicks (A chicks, 14.26 ± 1.44 g day^{-1}; B chicks, 13.2 ± 1.45 g day^{-1}; LMM; rank, $\chi^2_1 = 9.00$, $p = 0.003$; HA, $\chi^2_2 = 0.002$, $p = 0.96$; all other $p > 0.23$). Chick rank was also the only significant variable explaining variation in chicks' maximal structural size and body mass (all other $p > 0.27$). A chicks reached a significantly higher maximal structural size and body mass than B chicks (A chicks, maximal structural size of 5.29 ± 0.58 principal component analysis (PCA) units day^{-1} and maximal body mass of 408.75 ± 44.86 g; B chicks, maximal structural size of 5.15 ± 0.68 PCA units day^{-1}, LMM; rank, $\chi^2_1 = 10.51$, $p = 0.001$; maximal body mass of 389.63 ± 51.16 g, LMM; rank, $\chi^2_1 = 4.80$, $p = 0.028$). Hatching date had a negative effect on mass gain and maximal structural size (LMM; mass gain, $\chi^2_1 = 3.71$, $p = 0.054$; maximal structural size, $\chi^2_1 = 4.39$, $p = 0.036$).

Chick survival

The interaction between rank and HA was significantly related to chick survival (CPH mixed; $\chi^2_1 = 6.43$, $p = 0.011$, Fig. 5). The effect of HA on chick survival was reversed for A and B chicks. With HA increasing, B chicks survival prospects decreased significantly, whereas there was a slight increase of A

chicks survival (CPH; A chicks (HA, $\chi^2_1 = 2.14$, $p = 0.14$); B chicks (HA, $\chi^2_1 = 4.67$, $p = 0.03$), Fig. 5). Chicks born later in the season were also more likely to die (CPH mixed; $\chi^2_1 = 9.25$, $p = 0.002$).

Discussion

Among the hypotheses proposing adaptive benefits of HA in birds (Magrath 1990; Stenning 1996), the sibling rivalry hypothesis (Hahn 1981) has received among the more convincing experimental support (e.g. Mock and Ploger 1987; Gilby et al. 2011). This hypothesis states that HA facilitates the establishment of a within-brood dominance relationship, thereby helping to reduce energy wastage in sibling competition. Here, we experimentally manipulated HA magnitude both downward and upward in a facultatively siblicidal species to evaluate its consequences from hatching to fledging.

Overall, our experimental manipulation of HA magnitude seemed to confirm the sibling rivalry hypothesis (Hahn 1981). Brood-level competition (in terms of aggression, but not begging, see Gilby et al. 2011) generally decreased when the magnitude of HA increased and parents tended to feed synchronous broods more actively, although no benefits concerning maximal structural size or body mass were observed. Synchronous hatching may thus lead to higher costs and energy wastage for both chicks and parents, as shown by previous studies (e.g. Osorno and Drummond 1995; Gilby et al. 2011). At the individual level, our results confirm that A chick aggression rate increased with the magnitude of HA, leading to an exaggerated B chick mortality in highly asynchronous broods. Yet, contrary to previous studies (Mock and Ploger 1987), experimentally increased HA led to an increased begging frequency among B chicks. Overall, energetic costs triggered by synchronous hatching and increased B chick mortality in highly asynchronous broods together with lower aggression rate in broods with natural HA suggest that the natural situation may be optimal for parents. However, further studies are needed to confirm whether this is always true or dependent on environmental conditions (Lack 1947; Hahn 1981; see also Wiebe and Bortolotti 1994a). Particular focus should be put on the long-term fitness consequences for chicks and parents of the different magnitudes of HA (Mock and Forbes 1994; see also Mainwaring et al. 2012).

Chick behaviours

Our experimental manipulation of HA indicated that aggression frequency at the brood level had a quadratic relationship with HA before 10 days, with more aggressions occurring in very synchronous broods, as expected (e.g. Osorno and Drummond 1995; Viñuela 1999; Gilby et al. 2011) and, surprisingly, in highly asynchronous broods (Osorno and

Table 2 Generalised linear model selection to explain the variation in the rate at which the A chick displayed aggression, begging or feeding behaviours according to hatching asynchrony (HA), HA^2 and hatching date for the three different time periods

Variable removed from the complete model	Before 10 days			After 10 days			Overall		
	χ^2	df	p	χ^2	df	p	χ^2	df	p
Aggression									
HA^2	1.53	1	0.22	0	1	1	0.91	1	0.34
HA	**11.55**	**1**	**0.0007**	0	1	1	**8.58**	**1**	**0.003**
Hatching date	*3.25*	*1*	*0.07*	0	1	1	0.0008	1	0.97
		β	SE					β	SE
Selected model	(Intercept)	−0.32	0.48				(Intercept)	−0.04	0.45
	HA	1.37	0.58				HA	1.33	0.57
Begging									
HA^2	**3.65**	**1**	**0.05**	0.02	1	0.88	1.26	1	0.26
HA	1.93	1	0.16[a]	0.39	1	0.53	1.56	1	0.21
Hatching date	0.52	1	0.47	0.006	1	0.93	0.03	1	0.87
		β	SE						
Selected model	(Intercept)	−0.06	0.40						
	HA^2	−0.40	0.24						
	HA	0.83	0.68[a]						
Feeding									
HA^2	0.17	1	0.68	0.65	1	0.42	0.39	1	0.53
HA	0.0008	1	0.98	0.06	1	0.80	0.08	1	0.78
Hatching date	2.44	1	0.12	0.08	1	0.78	1.77	1	0.18

Significant terms are highlighted in bold, while marginally significant terms are highlighted in italic (but not retained in the selected model)

χ^2 chi-square value (change in deviance), *df* difference in degrees of freedom between the two models compared, *p* p value, β estimated coefficient, *SE* standard error of the estimated coefficient

[a] When HA^2 was significant, HA was retained in the model even if not significant
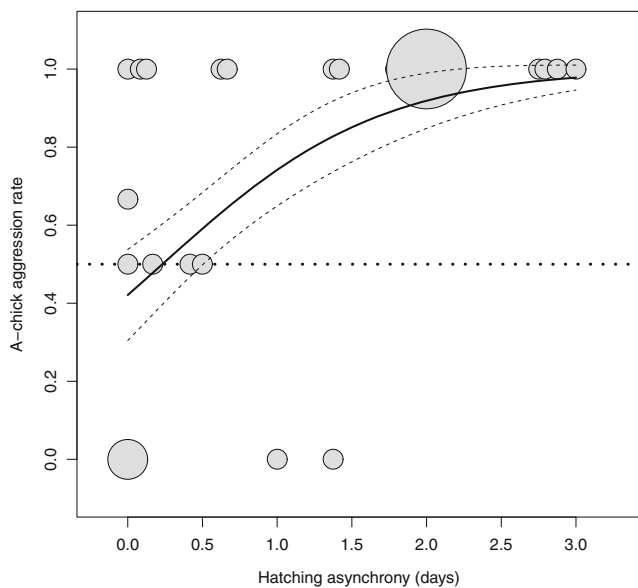

Fig. 2 The relationship between hatching asynchrony and A chick aggression rate during the first 10 days after B chick hatching. *Shaded dots* represent observed data (dot size proportional to the number of observations) from 26 nests where at least one chick was seen behaving aggressively toward the other. *Solid and dashed lines* are GLM predicted values and SE, respectively, whereas the *dotted line* represents a 50 % rate
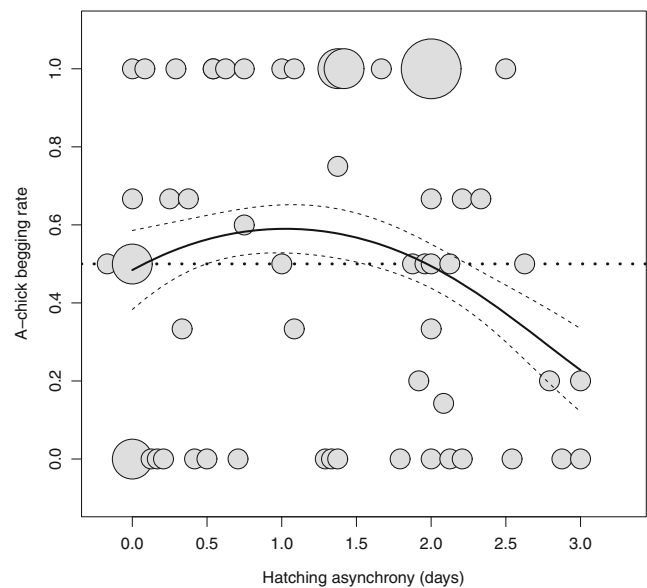

Fig. 3 The relationship between hatching asynchrony and A chick begging rate during the first 10 days after B chick hatching. *Shaded dots* represent observed data (dot size proportional to the number of observations) from 62 nests where at least one chick was seen begging. *Solid and dashed lines* are GLM predicted values and SE, respectively, whereas the *dotted line* represents a 50 % rate
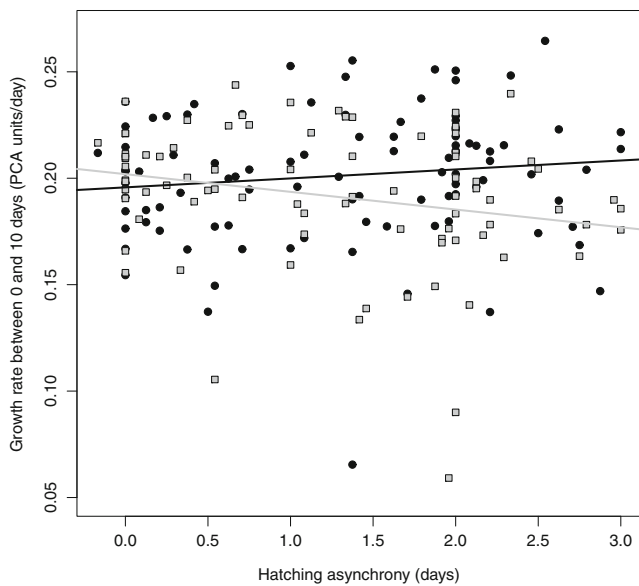
Fig. 4 Structural size growth rate between 0 and 10 days (PCA units/day) for A (*black dots*, N=98) and B chicks (*grey squares*, N=83), according to hatching asynchrony. *Lines* are linear regression predictions. Results were not affected when the four outliers with an extreme growth rate below 0.11 were removed

Drummond 1995; Viñuela 1999; but see Forbes 1991). This latter result echoes patterns observed in species with obligate siblicide, where HA is usually larger (e.g. Anderson 1989). However, aggression frequency tended to be linearly negative across the whole data set, which means that aggression was

Fig. 5 Survival probability according to chick age and hatching asynchrony (*solid lines* HA=0 days; *dashed lines* HA=1.5 days; *dotted lines* HA=3 days) for **a** A chicks and **b** B chicks. Although HA was analysed as a continuous variable (see text), it is displayed here as a categorical variable for illustrative purposes. B chick hatching date (i.e. a significant covariate) was held at its average value

very scarce in highly asynchronous broods after 10 days. Hence, once the dominance relationship was established, A chicks probably reduced their aggression rates, in line with the decrease we found in aggression frequency with chick age (see also Nathan et al. 2001). Sibling competition was thus higher in synchronous broods because both chicks were very aggressive toward each other during the whole period, suggesting an escalated conflict between size-matched individuals as predicted by game theory models (Maynard-Smith 1982). Interestingly, our analysis at the individual level highlighted that B chicks were slightly more aggressive than A chicks for small HA magnitudes, whereas A chicks were clearly more aggressive with increasing HA magnitude. Previous studies also found an increase of aggression frequency in synchronous broods (e.g. Mock and Ploger 1987; Osorno and Drummond 1995), but A chicks were always more aggressive than B chicks. In cattle egrets (*Bubulcus ibis*), A eggs contain more androgens (Schwabl 1997), and in blue-footed boobies (*Sula nebouxii*), there are no differences in androgen concentrations according to rank (Drummond et al. 2008). In kittiwakes, however, B eggs contain more androgens than A eggs (e.g. Vallarino et al. 2012; Benowitz-Fredericks et al. 2013), and these hormones have been shown to experimentally increase chick aggression and dominance (Müller et al. 2012). This might explain B chick behaviour when HA was very close to 0, despite their smaller size at hatching (Merkling et al. 2012). Altogether, these results confirm that asynchronous hatching favours within-brood hierarchy establishment and that A chicks need a substantial age/size advantage to become dominant, in accordance with the sibling rivalry hypothesis (Hahn 1981).
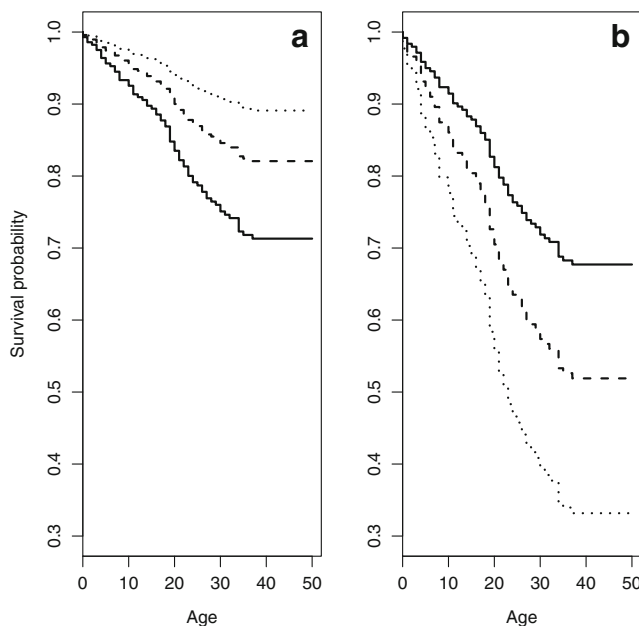
Begging frequency tended to increase with HA before 10 days at the brood level, contrary to the sibling rivalry hypothesis (Hahn 1981) and previous studies (Fujioka 1985; Gilby et al. 2011). For the same period, analyses at the individual level showed a significant quadratic relationship between HA and A chick begging rate. Consistent with previous findings in kittiwakes (Braun and Hunt 1983), A chicks begged slightly more than B chicks for HA magnitudes approximating the natural range. Yet, for HA magnitudes above about 2.2 days, B chicks begged significantly more than their siblings. Hence, the more B chicks faced a low growth rate, the more they begged, coherently with theoretical predictions of begging scramble models (Parker et al. 2002). As we did not record behavioural sequences, we were not able to determine whether B chick begging led to A chick aggression, as previously reported (e.g. Forbes 1991) and as it would be expected if A chicks were selected to increase their share of food available. However, our personal observations seem to corroborate these findings. Although high B chick begging could signal their higher hunger level to parents, we did not find any effect of HA magnitude on A chick feeding rate, in contradiction with previous studies (e.g. Osorno and

Drummond 1995; Gilby et al. 2011). This may suggest that B chicks needed to beg substantially more than A chicks to get the same amount of food and that begging became more costly for B chicks with increasing HA (Godfray 1995; Parker et al. 2002).

Moreover, in agreement with our predictions, we found that feeding frequency at the brood level tended to decrease with HA overall and after 10 days. In line with previous studies (e.g. Fujioka 1985; Mock and Ploger 1987; Wiehn et al. 2000), it seems that the increase in sibling competition, through aggression but not begging, arising from synchronous hatching forced parents to increase their feeding effort. Yet, parental compensation was delayed, as we did not detect any effect of HA on feeding frequency before 10 days. This increase in parental feeding frequency in synchronous broods as compared to more asynchronous broods could also be coherent with the non-mutually exclusive peak load reduction hypothesis (Hussell 1972; Mock and Schwagmeyer 1990). It states that HA could enable parents to reduce the maximum level of the brood's daily food requirements by offsetting the chicks' demand curves. However, no study found a strong support for this hypothesis despite many trials (e.g. Wiebe and Bortolotti 1994b; Siegel et al. 1999; Smiseth and Morgan 2009), and the long chick-rearing period in kittiwakes might prevent these selective pressures to occur in our species (Mock and Schwagmeyer 1990). Future studies should investigate the long-term effects on parental survival and reproduction of this increase in parental effort arising from synchronous hatching (Mock and Ploger 1987; Mock and Forbes 1994). Indeed, we would expect long-lived species, such as kittiwakes, to favour their survival and future reproductive attempts over current offspring and, therefore, to be reluctant to increase parental effort (Drent and Daan 1980; but see Leclaire et al. 2011).

Chick growth and survival

In accordance with our predictions, we found that the difference between A and B chicks in structural size growth rate increased with the magnitude of HA. A chicks grew at the same rate regardless of HA magnitude, whereas B chick growth was impaired by increasing HA. These results suggest that, contrary to previous findings (Viñuela 2000; Gilby et al. 2011), increased aggression in synchronous broods did not affect chick growth. However, asynchronous hatching, either natural or experimentally increased, negatively affected B chick structural size growth rate compared to synchronous broods, as previously found (Fujioka 1985; but see Osorno and Drummond 1995). It is unlikely that feeding differences were involved in the decline of B chick structural size growth rate, as we did not find any differences in A and B chicks feeding rates or frequencies before 10 days. Nonetheless, B chicks in asynchronous and highly asynchronous broods may

have faced a trade-off between growth and other activities. Indeed, a high begging frequency combined with the high frequency of aggression received may have been physiologically costly (Noguera et al. 2010; see also Parker et al. 2002). Regardless of the mechanisms explaining these differences in structural size growth rate during the first 10 days, HA magnitude did not alter the body size chicks reached before fledging. This is probably because structural size growth rate negatively affected B chick survival probability until fledging (CPH; $\chi^2_1 = 4.17$, $p = 0.04$), thus masking differences in growth rate found during the first 10 days.

Mass gain did not depend on HA magnitude in either A or B chicks, but the former gained more weight than the latter during the first 10 days, despite similar rates of A and B chicks feeding (see also Leclaire et al. 2011; but see White et al. 2010). In highly asynchronous broods, B chicks may gain less weight than A chicks because of the costs associated with their higher begging rate and aggressions they received. In experimentally synchronous broods, however, A and B chicks had similar levels of aggression and feeding, while the difference in mass gain held true. One possible explanation is that parents fed A chicks larger meals than B chicks. A chicks came from larger eggs (Braun and Hunt 1983; our unpublished data) and were, thus, naturally slightly larger than B chicks at hatching, even in synchronous broods. Parental favouritism toward the largest nestling in term of meal size has been experimentally demonstrated in zebra finches (Gilby et al. 2011). The difference in mass gain between ranks held true until fledging—A chicks were significantly heavier than B chicks, contrary to previous findings in natural broods (Merkling et al. 2012)—and no influence of HA magnitude was found. The combined results concerning maximal structural size and body mass confirm previous findings that HA magnitude does not influence fledging size and mass in species with a long rearing period (e.g. Osorno and Drummond 1995; Viñuela 1999).

HA magnitude did affect chick survival before fledging, in line with our prediction; A chick survival increased slightly with HA magnitude, whereas B chick survival significantly decreased with HA magnitude, as previously found (Mock and Ploger 1987; Osorno and Drummond 1995; Viñuela 1999). B chicks that were heavily attacked and begged frequently (i.e. in highly asynchronous broods) were more likely to die than B chicks in other brood types. Increased sibling competition in synchronous broods was deleterious to A chicks, as they were almost as likely to die as their siblings, in accordance with the sibling rivalry hypothesis (Hahn 1981). Survival costs thus increased more rapidly for B chicks than they decreased for A chicks with increasing HA. This is coherent with the asymmetric sibling rivalry hypothesis (Forbes and Glassey 2000), which states that the phenotypic handicap imposed upon subordinate chicks via HA should buffer dominant chicks from adverse conditions, as shown in red-winged blackbirds (*Agelaius phoeniceus*) (Forbes et al.

1997; Forbes 2011). Our results are also coherent with Lack's explanation that natural HA should facilitate the elimination of the weakest chick when needed (Lack 1954). However, the question remains whether parents are able to intervene in sibling competition to facilitate or to prevent siblicide. Most studies (e.g. Drummond et al. 1986; Mock and Parker 1997) have reported that parents did not interfere in chick aggression to change the outcome of sibling competition, but not all (e.g. Viñuela 1999; Wiebe and Bortolotti 2000). Kittiwake parents appear at times to interfere physically in sibling aggression by sitting on the chicks (authors personal observations), but an adaptive role of this behaviour has still to be proved. As A chicks were highly aggressive and B chicks had poor survival prospects in highly asynchronous broods, it is possible that a greater than natural HA magnitude can lead to a parental loss of control over brood reduction through siblicide (as defined by Mock 1994). Hence, the natural magnitude of HA may be adaptive in part because it moderates sibling competition and chick losses, as shown in our study, but also because it may give parents greater control over the outcome of sibling competition.

Ethical standards This experiment was conducted under the approval of the USGS Alaska Science Center Animal Care and Use Committee, the IPEV Ethical Committee, in accordance with U.S. laws and under permits from the U.S. Fish and Wildlife Service and the State of Alaska. Any use of trade names is for descriptive purposes only and does not imply endorsement of the U.S. Government.

References

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:3–4
Anderson DJ (1989) The role of hatching asynchrony in siblicidal brood reduction of two booby species. Behav Ecol Sociobiol 25:363–368
Barrett RT, Runde OJ (1980) Growth and survival of nestling kittiwakes *Rissa tridactyla* in Norway. Ornis Scand 11:228–235
Bates D, Maechler M, Bolker BM (2011) package "lme4": linear mixed-effects models using S4 classes (version 0.999375-42). http://cran.r-project.org/web/packages/lme4/index.html
Benowitz-Fredericks ZM, Kitaysky AS, Welcker J, Hatch SA (2013) Effects of food availability on yolk androgen deposition in the black-legged kittiwake (*Rissa tridactyla*), a seabird with facultative brood reduction. PLoS ONE 8:e62949
Blanchard P, Hanuise N, Dano S, Weimerskirch H (2007) Offspring sex ratio in relation to parental structural size and body condition in the long-lived wandering albatross (*Diomedea exulans*). Behav Ecol Sociobiol 61:767–773

Box G, Cox D (1964) An analysis of transformations. J R Stat Soc B Met 26:211–252
Braun BM, Hunt GLJ (1983) Brood reduction in black-legged kittiwakes. Auk 100:469–476
Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252
Drummond H (2006) Dominance in vertebrate broods and litters. Q Rev Biol 81:3–32
Drummond H, Gonzalez E, Osorno JL (1986) Parent–offspring cooperation in the blue-footed booby (*Sula nebouxii*): social roles in infanticial brood reduction. Behav Ecol Sociobiol 19:365–372
Drummond H, Rodriguez C, Schwabl H (2008) Do mothers regulate facultative and obligate siblicide by differentially provisioning eggs with hormones? J Avian Biol 39:139–143
Forbes LS (1991) Hunger and food allocation among nestlings of facultatively siblicidal ospreys. Behav Ecol Sociobiol 29:189–195
Forbes S (2011) Social rank governs the effective environment of siblings. Biol Lett 7:346–348
Forbes S, Glassey B (2000) Asymmetric sibling rivalry and nestling growth in red-winged blackbirds (*Agelaius phoeniceus*). Behav Ecol Sociobiol 48:413–417
Forbes S, Thornton S, Glassey B, Forbes M, Buckley NJ (1997) Why parent birds play favourites. Nature 390:351–352
Fujioka M (1985) Sibling competition and siblicide in asynchronously-hatching broods of the cattle egret *Bubulcus ibis*. Anim Behav 33:1228–1242
Gilby AJ, Mainwaring MC, Griffith SC (2011) The adaptive benefit of hatching asynchrony in wild zebra finches. Anim Behav 82:479–484
Gill VA, Hatch SA (2002) Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding. J Avian Biol 33:113–126
Gill VA, Hatch SA, Lanctot R (2002) Sensitivity of breeding parameters to food supply in black-legged kittiwakes *Rissa tridactyla*. Ibis 144:268–283
Godfray HCJ (1995) Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. Am Nat 146:1–24
Hahn DC (1981) Asynchronous hatching in the laughing gull: cutting losses and reducing rivalry. Anim Behav 29:421–427
Hamilton WD (1964) The genetical evolution of social behaviour. I. J Theor Biol 7:1–16
Hatch SA, Robertson GJ, Baird HP (2009) Black-legged kittiwake (*Rissa tridactyla*). The birds of North America online. Cornell Laboratory of Ornithology, Ithaca, NY
Hussell DJ (1972) Factors affecting clutch size in arctic passerines. Ecol Monogr 42:317–364
Irons DB (1992) Aspects of foraging behavior and reproductive biology of the black-legged kittiwake. University of California, Irvine
Lack D (1947) The significance of clutch-size. Ibis 89:302–352
Lack D (1954) The natural regulation of animal numbers. Oxford University Press, Oxford
Leclaire S, Helfenstein F, Degeorges A, Wagner RH, Danchin É (2010) Family size and sex-specific parental effort in black-legged kittiwakes. Behaviour 147:13–14
Leclaire S, Bourret V, Wagner RH, Hatch SA, Helfenstein F, Chastel O, Danchin É (2011) Behavioral and physiological responses to male handicap in chick-rearing black-legged kittiwakes. Behav Ecol 22:1156–1165
Magrath RD (1990) Hatching asynchrony in altricial birds. Biol Rev 65:587–622
Mainwaring MC, Blount JD, Hartley IR (2012) Hatching asynchrony can have long-term consequences for offspring fitness in zebra finches under captive conditions. Biol J Linn Soc 106:430–438
Maynard-Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge
Maynard-Smith J, Parker GA (1976) The logic of asymmetric contests. Anim Behav 24:159–175

Merkling T, Leclaire S, Danchin E, Lhuillier E, Wagner RH, White J, Hatch SA, Blanchard P (2012) Food availability and offspring sex in a monogamous seabird: insights from an experimental approach. Behav Ecol 23:751–758

Mock DW (1994) Brood reduction: narrow sense, broad sense. J Avian Biol 25:3–7

Mock DW, Forbes LS (1994) Life-history consequences of avian brood reduction. Auk 111:115–123

Mock DW, Parker GA (1997) The evolution of sibling rivalry. Oxford University Press, Oxford

Mock DW, Ploger BJ (1987) Parental manipulation of optimal hatch asynchrony in cattle egrets: an experimental study. Anim Behav 35:150–160

Mock DW, Schwagmeyer PL (1990) The peak load reduction hypothesis for avian hatching asynchrony. Evol Ecol 4:249–260

Müller MS, Roelofs Y, Erikstad KE, Groothuis TG (2012) Maternal androgens increase sibling aggression, dominance, and competitive ability in the siblicidal black-legged kittiwake (*Rissa tridactyla*). PLoS ONE 7:e47763

Nathan A, Legge S, Cockburn A (2001) Nestling aggression in broods of a siblicidal kingfisher, the laughing kookaburra. Behav Ecol 12:716–725

Noguera JC, Morales J, Pérez C, Velando A (2010) On the oxidative cost of begging: antioxidants enhance vocalizations in gull chicks. Behav Ecol 21:479–484

Osorno JL, Drummond H (1995) The function of hatching asynchrony in the blue-footed booby. Behav Ecol Sociobiol 37:265–273

Ostreiher R, Pruett-Jones S, Heifetz A (2012) Asymmetric contests at the nest. Behav Ecol Sociobiol 66:1237–1246

Parker GA, Royle NJ, Hartley IR (2002) Begging scrambles with unequal chicks: interactions between need and competitive ability. Ecol Lett 5:206–215

Podlas KA, Richner H (2013) The adaptive function of hatching asynchrony: an experimental study in great tits. Anim Behav 86:567–576

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ricklefs RE (1965) Brood reduction in the curve-billed thrasher. Condor 67:505–510

Roulin A, Dreiss AN (2012) Sibling competition and cooperation over parental care. In: Royle NJ, Smiseth PT, Kölliker M (eds) The evolution of parental care. Oxford University Press, Oxford, pp 133–149

Royle NJ, Hamer KC (1998) Hatching asynchrony and sibling size hierarchies in gulls: effects on parental investment decisions, brood reduction and reproductive success. J Avian Biol 29:266–272

Schwabl H (1997) A hormonal mechanism for parental favouritism. Nature 386:231

Siegel RB, Weathers WW, Beissinger SR (1999) Hatching asynchrony reduces the duration, not the magnitude, of peak load in breeding green-rumped parrotlets (*Forpus passerinus*). Behav Ecol Sociobiol 45:444–450

Smiseth PT, Morgan K (2009) Asynchronous hatching in burying beetles: a test of the peak load reduction hypothesis. Anim Behav 77:519–524

Stearns S (1992) The evolution of life histories. Oxford University Press, Oxford

Stenning MJ (1996) Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. Trends Ecol Evol 11:243–246

Therneau T (2012) coxme: mixed effects Cox models. R package version 2.2-3. http://cran.r-project.org/web/packages/coxme/index.html

Vallarino A, Evans N, Daunt F, Wanless S, Nager R (2012) Egg components vary independently of each other in the facultative siblicidal black-legged Kittiwake *Rissa tridactyla*. J Ornithol:1–11

Venables WN, Ripley BD (2002) Modern applied statistics with S. Springer, New York

Viñuela J (1999) Sibling aggression, hatching asynchrony, and nestling mortality in the black kite (*Milvus migrans*). Behav Ecol Sociobiol 45:33–45

Viñuela J (2000) Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. Behav Ecol Sociobiol 48:333–343

White J, Leclaire S, Kriloff M, Mulard H, Hatch SA, Danchin E (2010) Sustained increase in food supplies reduces broodmate aggression in black-legged kittiwakes. Anim Behav 79:1095–1100

Wiebe KL, Bortolotti GR (1994a) Food supply and hatching spans of birds: energy constraints or facultative manipulation. Ecology 75:813–823

Wiebe KL, Bortolotti GR (1994b) Energetic efficiency of reproduction: the benefits of asynchronous hatching for American kestrels. J Anim Ecol:551–560

Wiebe KL, Bortolotti GR (2000) Parental interference in sibling aggression in birds: what should we look for? Ecoscience 7:1–9

Wiehn J, Ilmonen P, Korpimäki E, Pahkala M, Wiebe KL (2000) Hatching asynchrony in the Eurasian kestrel *Falco tinnunculus*: an experimental test of the brood reduction hypothesis. J Anim Ecol 69:85–95

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am Nat 100:687–690