

Family size and sex-specific parental effort in black-legged kittiwakes

**Sarah Leclaire^{1,2,3,5)}, Fabrice Helfenstein⁴⁾, Anne Degeorges^{1,2)},
Richard H. Wagner³⁾ & Étienne Danchin^{1,2)}**

(¹ CNRS, UPS, EDB (Laboratoire Évolution et Diversité Biologique), UMR 5174, 118 route de Narbonne, F-31062 Toulouse, France; ² Université de Toulouse, EDB (Laboratoire Évolution et Diversité Biologique), UMR 5174, 118 route de Narbonne, F-31062 Toulouse, France; ³ Konrad Lorenz Institute for Ethology, Savoyenstrasse 1a, A-1160 Vienna, Austria; ⁴ Evolutionary Ecology Group, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland)

(Accepted: 12 October 2010)

Summary

Clutch and brood reduction is widespread in birds and is mainly caused by lower parental effort during incubation or chick rearing. In black-legged kittiwakes *Rissa tridactyla*, early chick rearing seems to be more costly for females than males. We, thus, hypothesized that energetically constrained females may be responsible for the low feeding delivery causing brood-reduction. Furthermore, as previous studies have experimentally shown that only females reduce their feeding effort after brood-reduction, we hypothesized that females should decrease their investment after natural clutch or brood reduction. For three consecutive years, we observed parental attendance and feeding behaviour during chick rearing in pairs that hatched only one of their eggs, lost one of their two hatchlings or raised two chicks. We found that in pairs that lost one egg, parents behaved as predicted, with females showing low feeding effort. Furthermore, we found that before brood-reduction, females, but not males delivered less food to their chicks than parents that raised two chicks, and that A-chicks were more aggressive when females delivered less food to them. These results suggest that females may be responsible for brood-reduction. However, after brood-reduction, contrary to what was expected, females did not show lower feeding rate than females raising two chicks. We discuss two non-exclusive potential mechanisms at the origin of this result, namely that brood-reduction may be due to (i) low quality females that are not able to feed their two chicks enough or to (ii) females that adaptively restrained their feeding effort to maximize their residual reproductive value.

⁵⁾ Corresponding author's e-mail address: sarah.leclaire@free.fr

Keywords: black-legged kittiwakes, brood reduction, clutch reduction, feeding rate, parental effort, *Rissa tridactyla*

Introduction

Parents of numerous species showing parental care often produce more zygotes than they can raise (Lack, 1947, 1954; Kozłowski & Stearns, 1989). This may imply some secondary adjustments of family size (Mock & Forbes, 1995; Mock & Parker, 1998). In birds, the reduction in the number of young raised occurs in many species where it can take various forms and occur at different stages of reproduction. Before egg laying, females in poor condition may reduce their clutch size by follicular atresia (Hamann et al., 1986). During incubation, females may remove one of their eggs when facing adverse conditions (e.g., pied flycatcher, *Ficedula hypoleuca*; Lobato et al., 2006). In some penguins, parents always eject the smaller first-laid egg just before laying the second egg (St. Clair et al., 1995). Parents may also neglect or abandon the incubation of the last-laid egg after partial hatching of the clutch (Kloskowski, 2003). Finally, brood reduction may occur after hatching. The latter strategy has been intensively studied (Mock & Parker, 1997). For instance, in few species, parents may directly kill one of their chicks (Urrutia & Drummond, 1990; Zielinski, 2002). Hatching asynchrony and intraclutch variation in egg mass or hormonal titer can also facilitate brood reduction through a higher competitive ability of the stronger chick (Lack, 1947; Magrath, 1990; Stoleson & Beissinger, 1997; Drummond, 2001a; Groothuis et al., 2005). Finally, in some species, a decrease of parental feeding rate during food shortage, often linked to differential feeding rates towards individual chicks, may lead to siblicide (i.e., fatal sibling aggression; Drummond, 2001a).

Because of anisogamy, or more generally differential investments by the sexes, it has generally been assumed that brood size adjustment is mainly under female control (Trivers, 1972). Only ova contain reserves and in species with internal fertilization, embryo development begins within female reproductive tracts. Egg size, hatching asynchrony as well as egg composition (e.g., presence of antibodies, hormones, lipids, proteins, etc.) depend on the mother's phenotype (e.g., size, age, body condition, social rank; Gasparini et al., 2002; Groothuis et al., 2005; Tanvez et al., 2008; Beamonte-Barrientos et al., 2010) in interaction with current environmental conditions (e.g., food

availability, quality of the mate; Wiebe & Bortolotti, 1994; Velando et al., 2006). Males, in contrast, are supposed to have little control over such early breeding parameters. Brood reduction caused by poor egg quality or initial competitive asymmetry between brood mates is, thus, usually considered as mainly under female control. However, because more than 90% of avian species exhibit biparental care (Lack, 1968; Bennett & Owens, 2002), secondary brood size adjustment may also involve males.

How much males and females vary in the level of care provided to their nestlings is a central question in behavioural ecology (e.g., Lombardo, 1991; Carere & Alleva, 1998; Sanz et al., 2000; Dawson & Bortolotti, 2003; Quillfeldt et al., 2004; Dickens & Hartley, 2007). Patterns of parental investment may be determined by a combination of factors, such as variation in the response to chick begging, differences in foraging efficiency and competitive ability, or sexual conflict (Gonzalez-Solis et al., 2000; Lewis et al., 2002; Quillfeldt et al., 2004; Lessells, 2006). In this context, the adaptive value of clutch and brood reduction likely varies between the sexes. Since Trivers' seminal paper on parental investment (Trivers, 1972), it has been generally suggested that the sex which undergoes the greater cost of care may be selected to allocate care more selectively and, thus, to be more prone to promote a reduction in family size.

The black-legged kittiwake (*Rissa tridactyla*) is a socially and genetically monogamous species (Helfenstein et al., 2004) with high parental effort by both sexes (Coulson, 1966; Coulson & Johnson, 1993). Males compete for nest sites, participate in nest building, provide most of the food to females during egg formation and share incubation and parental care with their mates (Helfenstein et al., 2003). Most females lay two eggs. However, in some years, a significant proportion of the pairs lose either one egg or one chick before fledging. Egg loss or hatching failure may have many causes (e.g., predation, low environmental food availability, inbreeding depression, sperm age; Massaro et al., 2000; Gill & Hatch, 2002; White et al., 2008; Mulard et al., 2009) but has been poorly investigated and the relative influence of female quality compared to environmental factors is unknown. Regarding brood reduction, it is mainly caused by siblicide, which is due to low parental feeding rate when environmental food availability is low (Braun & Hunt, 1983; Irons, 1992; White et al., 2010). The bulk of brood reduction occurs during the first part of chick rearing, i.e., at a time that is energetically demanding, especially for females (Moe et al., 2002). During this period, adults cannot leave the chicks alone. Their energy intake does not meet

their energy requirements and they lose mass, especially females (Moe et al., 2002). Furthermore, females tend to have a higher field metabolic rate than males, whereas they do not attend the nest more than males. This suggests that work effort could be higher in females than males (Fyhn et al., 2001). Additionally, only females seem to decrease their parental effort after experimental brood reduction (Jacobsen et al., 1995), which may suggest that females may benefit from brood reduction more than males. Hence, we assumed that females may be the sex responsible for the low feeding delivery leading to brood reduction in kittiwakes.

Here we report on a study of parental effort during chick rearing in unmanipulated black-legged kittiwake pairs. We compared parental effort during the early chick rearing period in pairs that hatched only one of two eggs, lost one of their two hatchlings or raised two chicks. We aimed at testing the hypothesis that brood reduction in kittiwakes is primarily caused by females as a mean to lower their investment in current reproduction. We predicted that before brood reduction, females that lost one hatchling would feed their chicks at a lower rate than females that raised two chicks. Furthermore, because only females were found to adjust their effort to an experimental decrease in brood size (Jacobsen et al., 1995), we expected male investment to remain unchanged after natural clutch or brood reduction, whereas females were expected to adjust their investment just after losing one egg or chick. Finally, to assess how parents respond to clutch and brood reduction in a longer term, we investigated parental effort during the late rearing period (from day 14 to day 30 post-hatch).

Methods

Study site

The study was carried out in Cap Sizun, Brittany, France (48°5'N, 4°36'W), where more than 15 000 kittiwakes have been colour-ringed and monitored since 1979. E.D. had a French full ringing license delivered by the French Ringing Center (CRBPO in the Museum of Paris). Ringers use rope-access techniques to access nests, chicks and adults. Effort is made to specifically ring chicks from parents of known pedigree. Birds are captured only once in their lifetime in order to minimize disturbance. Colour rings are made

of 1-mm-thick Darvic. All methods are fully registered in the French ringing scheme. Our observations were made on one cliff, which had over 250 breeding pairs in each study year. Kittiwakes were observed with binoculars from the opposite side of the gully about 30 m away. This meant no disturbance and all nests could be simultaneously monitored. We observed chick feeding in 1999, 2000 and 2001, parental attendance in 1999 and 2000 and sibling aggression in 2000.

Data collection and convention

Behaviour was recorded from pairs that had reached the chick rearing stage and with at least one individually colour-ringed parent. Wing patterns were registered for all individuals in the sample using Cadiou's (1993) method, which allowed us to recognise every breeder even when rings were not visible. The patterns of black and white dots at the extremity of the wing feathers are very easily observed even from 30 m away, and have been shown to be highly variable across individuals and consistent between years within individuals (Cadiou, 1993).

Chick feeding was monitored by continuous sampling (Altmann, 1974) and was recorded for 92 pairs (30 pairs in 1999, 37 pairs in 2000 and 25 pairs in 2001). Observations were made every day at randomly chosen times in the day (from 9 a.m. to 10.30 p.m.). The total time spent daily in observation ranged from 1 h 10 min to 7 h (mean 3 h 40 min, total 429 h 40 min). A parent was considered feeding its chick(s) when we could see the food item pass on from the parent to the chick, when a chick pecked inside its parent's beak or when a chick made visible efforts to swallow a bolus. We defined parental feeding frequency as the number of feeding bouts per hour. A feeding bout started when the chick(s) started to beg for food and ended once the chick(s) received food and stopped begging, and the parent stopped making any visible movements to regurgitate food. In 2000, the amount of food received by each chick (i.e., first- and second-hatched chicks (A- and B-chicks, respectively)) was also recorded. Bolus size was measured using the following scores: 1 for small bolus size, 2 for medium bolus size, and 3 for large bolus size. In practice, a small bolus was less than the size of the chick's bill (small bits of digested fish), a medium bolus was roughly the size of the chick's bill, necessitating some head movements to swallow the bolus, and a large bolus was bigger than the size of the chick's bill (e.g.,

a whole undigested fish) necessitating visible efforts to swallow the bolus. We defined the quantity of food as the sum of bolus sizes per hour. The quantity of food was defined as zero when there was no feeding bout during the whole time of observation. F.H. was assisted by one or two observers to record feeding behaviour. All observers were trained by F.H. to accord on estimation of bolus size.

Sibling aggression was recorded in 2000. A chick was considered to show aggressive behaviour when it pecked at its sibling. We defined aggression frequency as the number of aggression bouts per hour.

Nest attendance was recorded for 38 pairs in 1999 and 2000 by instantaneous scan sampling (Altmann, 1974), one to four times a day, at random times, with a minimum interval of one hour between scans. The total number of scans was 1702 nest scans (mean 2.57 scans/day) in 1999 and 1816 nest-scans (mean 2.33 scans/day) in 2000. Scans recorded the presence or absence of males and females. We defined male and female attendance as the daily proportion of time they were seen on the nest.

Breeding sites were inspected daily with binoculars from the opposite side of the gully to determine laying date, clutch size, hatching date, number of hatched chicks, date of chick loss, fledging date and number of fledged chicks. Kittiwake chicks always hatch asynchronously (minimal 1 day between the A- and B-chick hatching), which enables the identification of the first hatched chick as the biggest chick. Adult sexing was based on copulation and courtship feeding during the pre-laying period.

Data analysis

Analyses were performed on two egg broods and comprised those where (i) only one of the two eggs hatched (i.e., 'Clutch-reduction' broods), (ii) one of the two chicks died during the first 11 days (i.e., 'Brood-reduction' broods) and (iii) the two chicks fledged (i.e., '2-chick' broods). Broods where only one (6 monitored nests, 4.6%) or three eggs were laid (1 monitored nest, 0.8%) were excluded because sample sizes were too small for statistical analyses. Most brood reductions in kittiwakes occur during the first part of chick rearing when it is mainly due to siblicide (Braun & Hunt, 1983). Late brood reductions were scarce and often resulted from accidental falls. Only early brood reduction may hence be caused by low parental effort. In our study, 83% of brood reductions occurred during the first 15 days after the hatching of the second egg. Thus, we considered only brood reduction occurring before 15 days.

We first compared male and female behaviour (feeding frequency and parental attendance) before and after brood reduction between clutch-reduction or brood-reduction broods and 2-chick broods during the first 13 days of chick rearing. Because day 7 after hatching corresponds to the average date of brood reduction, we used that day as a surrogate cut-off between before and after brood reduction for clutch-reduction and 2-chicks groups. In 1999 and 2001, no distinction was made between food deliveries to A- and B-chicks. Feeding frequency was, thus, expressed as total feeding frequency and not as per capita feeding frequency. We used generalized linear mixed models (GLMM) to test differences between groups in the square-root transformed feeding frequency and non-transformed attendance. Fixed effects were Parental Sex, Period (before vs. after brood reduction or before vs. after day 7 post-hatch) and Brood group (clutch-reduction, brood-reduction, or 2-chicks). The nest (nested within Brood group), the year and the interaction between Period and nest (nested within Brood group) were entered as random effects. Individual-identity (nested within nest) was entered as the random subject to conduct a repeated-measure analysis where Period was a time effect (Littell et al., 2006). This allowed us to investigate how feeding frequency varied within individuals from before to after brood reduction or from before to after day 7 post-hatch.

In 2000, too few clutch-reduction broods were observed to be included in the feeding quantity analyses. The quantity of food was recorded separately for A- and B-chicks. We, thus, investigated how the quantity of food per hour delivered by males and females to A-chicks varied according to Brood group (2-chick or brood-reduction) and Period. We used the same model as for feeding frequency. B-chicks only survived in 2-chick broods and, thus, we investigated how the quantity of food per hour delivered by males and females to B-chicks before brood reduction varied according to Brood group (2-chick or brood-reduction), through *t*-tests. Food quantity delivered per hour was square-root transformed. The relationship between food quantity delivered to A-chick by males or females, and chick aggression was analysed through Pearson correlation tests. The difference in aggression between brood-reduction and 2-chick broods was analysed through *t*-tests.

In a second analysis, we compared male and female behaviour between 1-chick or brood-reduction broods and 2-chick broods from day 14 to 30 of chick-rearing. We used GLMMs to investigate how the square-root transformed feeding frequency or parental attendance varied according to Parental

Sex and Brood group. The nest (nested within Brood group) and the year were entered as random effects.

Analyses were conducted with the SAS system version 9.1. All GLMMs assumed normal distribution of the error and used the restricted maximum likelihood estimation method (REML-GLMMs) and the Satterthwaite correction for the calculation of fixed effects degrees of freedom (Littell et al., 2006). We checked the fit of our model by testing residuals for normality and homoscedasticity and by plotting the studentised residuals against the predicted values. Model selection was carried out by removing, one by one, the effects that were the furthest from statistical significance, starting with the highest order interactions down to the main effects. We used two-tailed type-3 tests for fixed effects with a significance level set to $\alpha = 0.05$. Values are expressed as mean \pm SE throughout.

Results

Brood-reduction vs. 2-chick parents

In 1999, brood reduction was observed in fewer broods than in 2000 and 2001 (38, 61 and 54% of broods that initially comprised two chicks; $\chi^2_2 = 6.0$, $p = 0.05$). Furthermore, before brood reduction, females fed their chicks at a higher rate in 1999 than in 2000 and 2001 ($F_{2,38} = 4.13$, $p = 0.024$; 0.27 ± 0.09 bouts/h, 0.12 ± 0.02 bouts/h and 0.13 ± 0.02 bouts/h respectively; 1999 vs. 2000: $p = 0.0076$, $\alpha = 0.017$, 1999 vs. 2001: $p = 0.024$, $\alpha = 0.025$). Compared to 2000 and 2001, 1999 seems, thus, a special year in terms of brood reduction and we performed two different analyses to test a difference between brood-reduction and 2-chick parental behaviour. One analysis was performed with the 1999 data and the other analysis with the 2000 and 2001 data together. Laying date was not different between brood-reduction and 2-chick broods ($F_{1,77} = 0.00$, $p = 0.98$).

In 2000 and 2001, between day 0 and day 13 post-hatch, feeding rate depended upon the triple interaction between Brood-group, Sex and Period ($F_{1,48.2} = 4.68$, $p = 0.036$, Figure 1). In females, feeding rate depended upon the interaction between Brood-group and Period ($F_{1,53.9} = 5.86$, $p = 0.019$). Before brood reduction or day 7, brood-reduction females fed their chicks at a lower rate than 2-chick females ($F_{1,55} = 5.32$, $p = 0.025$). After brood reduction or day 7, only 2-chick females decreased their feeding rate

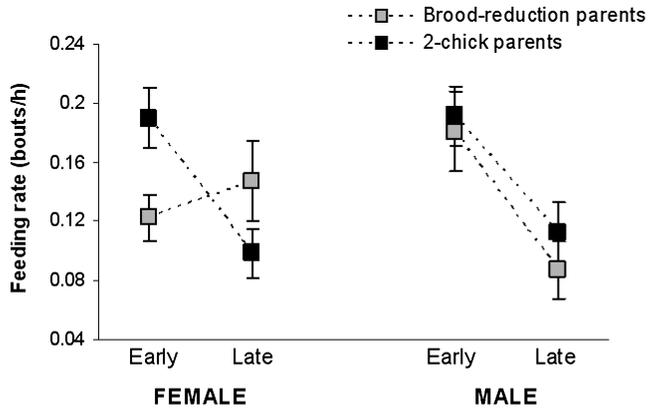


Figure 1. Female and male feeding rate (bouts/h) between hatching and brood reduction (early) and between brood reduction and day 13 post-hatch (late) in brood-reduction nests (grey, $N = 35$) and between hatching and day 6 post-hatch (early) and between day 7 and day 13 post-hatch (late) in 2-chick broods (black, $N = 23$). Shown are means \pm SE of 2000 and 2001 data.

($F_{1,22} = 12.84$, $p = 0.0017$), so that they fed their chicks at the same rate as brood-reduction females ($F_{1,55.2} = 1.48$, $p = 0.23$). In males, feeding rate decreased after brood reduction or day 7 ($F_{1,54.9} = 26.23$, $p < 0.001$) but it did not depend upon Brood-group ($F_{1,54.1} = 1.47$, $p = 0.23$).

Brood-reduction females delivered a lower amount of food to A-chick than 2-chick females ($F_{1,38.9} = 5.60$, $p = 0.023$, Figure 2) whereas brood-reduction males delivered the same amount of food to A-chicks than 2-chick males ($F_{1,38.9} = 0.54$, $p = 0.47$, Figure 2). Food amount delivered by males and females did not depend upon Period ($F_{1,39} = 0.69$, $p = 0.41$ and $F_{1,39.2} = 2.17$, $p = 0.15$, respectively; Figure 2). Food amount delivered to B-chick was not significantly different between brood-reduction and 2-chick broods (males: 0.04 ± 0.01 bolus size/h vs. 0.08 ± 0.04 bolus size/h; $t_{39} = 1.27$, $p = 0.21$, females: 0.04 ± 0.02 bolus size/h vs. 0.04 ± 0.02 bolus size/h; $t_{39} = 0.34$, $p = 0.74$).

Aggression frequency was correlated to the food amount delivered to A-chicks by females ($r^2 = -0.21$, $p = 0.0023$, $N = 41$; Figure 3), but was not correlated to the food amount delivered by males ($r^2 = -0.01$, $p = 0.49$, $N = 41$; Figure 3). Aggression frequency was not significantly different between brood-reduction and 2-chick broods (0.11 ± 0.01 bouts/h vs. 0.09 ± 0.02 bouts/h; $t_{39} = -0.75$, $p = 0.46$).

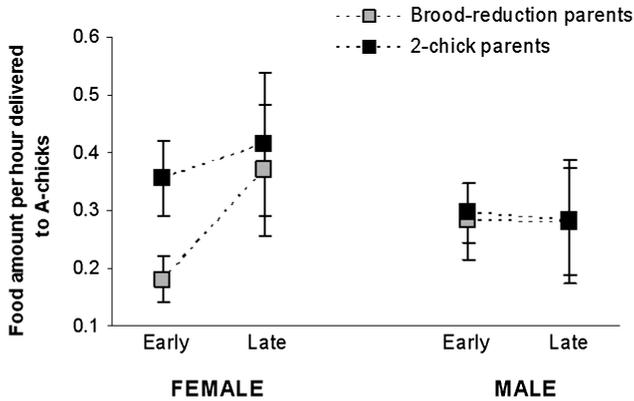


Figure 2. Quantity of food delivered per hour to A-chick by females and males, between hatching and brood reduction (early) and between brood reduction and day 13 post-hatch (late) in brood-reduction nests (grey, $N = 27$) and between hatching and day 6 post-hatch (early) and between day 7 and day 13 post-hatch (late) in 2-chick broods (black, $N = 14$). Shown are means \pm SE of 2000 data.

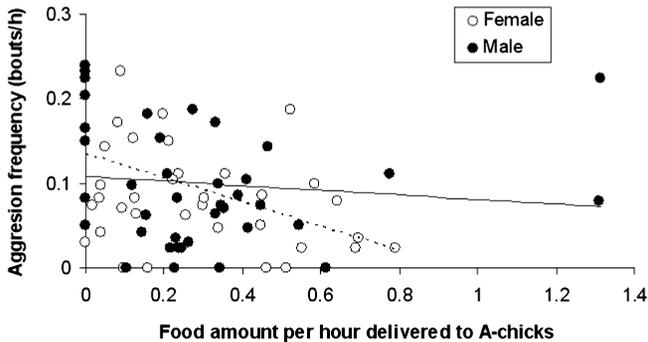


Figure 3. Sibling aggression frequency in relation to food amount delivered per hour to A-chick by males (black dots and continuous line) and females (white dots and dotted line), before brood-reduction or day 7. Shown are means \pm SE of 2000 data.

Between day 0 and day 13 post-hatch, parents almost never left chicks unattended (0.4% of observations) and almost no squatters (i.e., birds attending a nest where they did not breed that year; Monnat et al., 1990) were observed on the nests (0.3% of observations). Furthermore, males and females were almost never seen attending the nest together (0.5% of observations). In 2000, between day 0 and day 13 post-hatch, nest attendance did not depend upon Brood-group ($F_{1,63} = 0.05$, $p = 0.82$) or Period ($F_{1,67} = 0.32$, $p = 0.57$; nest attendance was not recorded in 2001). Nest at-

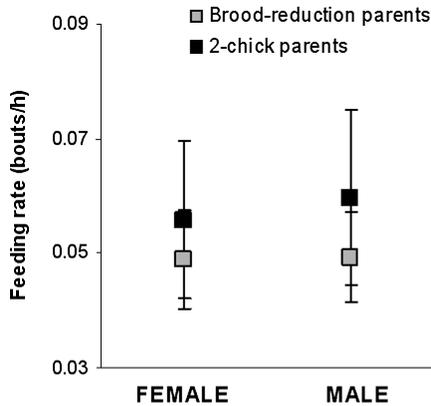


Figure 4. Feeding rate in females and males, in brood-reduction (grey, $N = 33$) and 2-chick (black, $N = 20$) nests between day 14 and day 30 post-hatch. Shown are means \pm SE of 2000 and 2001 data.

tendance was slightly higher in males than in females ($52 \pm 2\%$ and $48 \pm 2\%$), although it was non-significant ($F_{1,66} = 2.84$, $p = 0.097$).

Between day 14 and 30 of chick-rearing, feeding rate was slightly lower in brood-reduction group than in 2-chick group (Figure 4), but it was not significant ($F_{1,51} = 1.79$, $p = 0.19$). Feeding rate did not depend upon Sex ($F_{1,52} = 0.32$, $p = 0.57$, Figure 3). During this period, males and females attended their nests similarly ($F_{1,33} = 0.00$, $p = 0.98$), but they ceased attending the nest continuously. Brood-reduction parents almost never left their chick alone, whereas 2-chick parents left their chicks alone more often ($6 \pm 2\%$ and $32 \pm 7\%$, $F_{1,32} = 17.23$, $p = 0.0002$).

In 1999, between day 0 and day 13 post hatch, feeding rate did not depend upon Sex or Brood-group but all parents decreased their feeding rate after brood reduction or day 7 (before brood reduction or day 7: 0.18 ± 0.02 bouts/h vs. after brood reduction or day 7: 0.11 ± 0.01 bouts/h, $F_{1,47} = 8.47$, $p = 0.0055$). Nest attendance was higher in males than in females ($53 \pm 3\%$ and $46 \pm 3\%$, $F_{1,42} = 5.43$, $p = 0.025$) but it did not depend upon Brood-group ($F_{1,41} = 0.00$, $p = 0.95$) or Period ($F_{1,43} = 0.04$, $p = 0.84$). Between day 14 and 30 of chick-rearing, brood-reduction parents fed their single chick at a lower rate than 2-chick parents (0.07 ± 0.01 bouts/h and 0.11 ± 0.01 bouts/h, $F_{1,22} = 7.04$, $p = 0.015$), and feeding rate did not depend upon Sex ($F_{1,23} = 0.91$, $p = 0.35$). During this period, males and females attended their nests similarly ($F_{1,21} = 0.12$, $p = 0.74$), but they ceased attending the nest continuously. Brood-reduction parents almost never left their chick

alone, whereas 2-chick parents tended to leave their chicks alone more often ($6 \pm 3\%$ and $22 \pm 4\%$, $F_{1,20} = 4.11$, $p = 0.056$).

Clutch-reduction vs. 2 chick parents

Neither clutch reduction nor feeding rate between day 0 and day 7 post-hatch of 1-chick and 2-chick parents depended upon Year (clutch reduction rate in clutches that initially comprised 2 eggs: 22% in 1999, 18% in 2000 and 26% in 2001). Consequently, to test a difference between clutch-reduction and 2-chick parental behaviour, we gathered the 1999, 2000 and 2001 data in one analysis. Laying date was not different between 1-chick and 2-chick broods ($F_{1,52} = 0.05$, $p = 0.83$).

Between day 0 and 13 post hatch, feeding rate depended upon the interaction between Brood-group and Sex ($F_{1,52.4} = 5.55$, $p = 0.022$, Figure 5). Clutch-reduction females fed their chick at a lower rate than 2-chick females ($F_{1,52.9} = 13.43$, $p = 0.0006$) whereas clutch-reduction males fed their chick at the same rate as 2-chick males ($F_{1,54} = 0.39$, $p = 0.53$). Clutch-reduction and 2-chick parents decreased their feeding rate after day 7 post-hatch ($F_{1,54.2} = 24.63$, $p < 0.0001$). Between day 0 and 13 post-hatch, males attended the nest more often than females ($54 \pm 2\%$ and $45 \pm 2\%$, $F_{1,64} = 8.40$, $p = 0.0051$). Nest attendance depended neither upon Brood-group ($F_{1,63} = 0.05$, $p = 0.82$) nor Period ($F_{1,65} = 0.56$, $p = 0.46$).

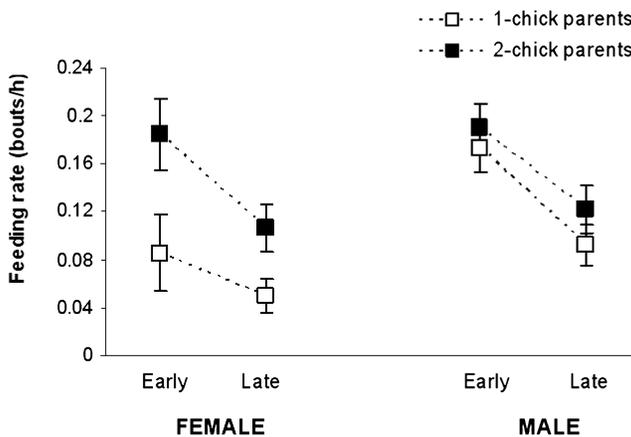


Figure 5. Male and female feeding rate in clutch-reduction (white, $N = 16$) and 2-chick (black, $N = 40$) nests, between hatching and day 7 post-hatch (early) and between day 7 and day 13 post-hatch (late). Shown are means \pm SE of 1999, 2000 and 2001 data.

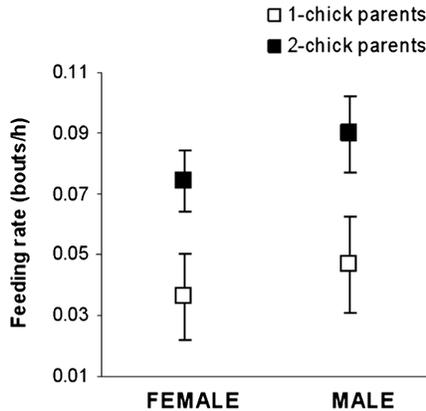


Figure 6. Female and male feeding rate in clutch-reduction (white, $N = 16$) and 2-chick (black, $N = 37$) nests between day 14 and day 30 post-hatch. Shown are means \pm SE of 1999, 2000 and 2001 data.

Between day 14 and 30 of chick-rearing, 2-chick parents fed their chicks at a higher rate than clutch-reduction parents ($F_{1,51} = 8.09$, $p = 0.0064$, Figure 6). Feeding rate did not depend upon Sex ($F_{1,52} = 2.35$, $p = 0.13$, Figure 5). Between day 14 and 30 of chick-rearing, males and females attended their nests similarly ($F_{1,32} = 0.10$, $p = 0.76$), but they ceased attending the nest continuously. Clutch-reduction parents almost never left their chick alone whereas 2-chick parents left their chicks alone more often ($3 \pm 2\%$ and $27 \pm 4\%$, $F_{1,31} = 6.36$, $p = 0.018$).

Discussion

In agreement with our expectations we found that females that hatched only one of their two eggs fed their single chick at lower frequencies than parents of two-chick broods. Furthermore, although a baseline level of brood reduction does not seem to be due to food delivery, we found that, in years when brood reduction rate is high, females but not males of brood-reduction pairs made fewer deliveries and fed their chicks with smaller bolus sizes, hence probably triggering brood reduction. However, contrary to our expectations, after brood reduction, females of brood-reduction pairs did not feed their single chick at a lower rate than parents whose two chicks survived to fledging. These results raise the question of the cause and potential benefits of clutch and brood reduction in this long-lived bird with shared parental investment.

Clutch reduction

As expected from results of a previous study (Jacobsen et al., 1995) or from the fact that egg failure depends mainly on mother quality, we found that during the early period of chick rearing, females that hatched only one of their two eggs fed their single chick at a lower frequency than females with two chicks whereas males of these two categories of breeders fed their chick(s) at similar frequencies (Figure 5). We also found that males and females that lost one egg showed similar nest attendance than males and females of pairs raising two chicks. This may result from two non-exclusive mechanisms.

During the first part of chick rearing, although their requirements are quantitatively lower, chicks are in constant need of care. This diminishes the amount of time available for foraging, and increases parental energy expenditure (Moe et al., 2002). In kittiwakes, as in wandering albatrosses *Diomedea exulans* (Salamolard & Weimerskirch, 1993), this period is probably more energetically demanding than the second part of chick rearing, when parents can leave the nest for long foraging trips (Moe et al., 2002). In kittiwakes, this high early breeding cost seems to differ between the sexes. Rearing females lose more weight than males (Golet et al., 1998; Moe et al., 2002) and tend to consume more energy (Fyhn et al., 2001; Jodice et al., 2006). If the cost of early care is greater for females than males, then female kittiwakes may be selected to allocate care more precisely than males. They are, thus, expected to adopt a 'flexible investment strategy' by adjusting their investment to chick requirements (e.g., as in puffin, *Fratercula artica*, Johnsen et al., 1994; female blue-footed booby, *Sula nebouxii*, Velando & Alonso-Alvarez, 2003; female Manx shearwater, *Puffinus puffinus*, Quillfeldt et al., 2004). Male kittiwakes were expected not to adjust their effort to brood size, as we found. They, thus, seem to follow a 'fixed investment strategy' and work at high physiological levels, as found in other seabirds (Leach's storm-petrel, *Oceanodroma leucorhoa*, Mauck & Grubb, 1995; male blue-footed booby, Velando & Alonso-Alvarez, 2003; male Manx shearwater, Quillfeldt et al., 2004). This hypothesis is supported by the fact that in kittiwakes, artificial brood reduction increases female, but not male body condition suggesting that only females adjust their effort to chick demand (Jacobsen et al., 1995). However, during the second part of chick rearing (from day 14 to day 30 post-hatch), males that lost one egg fed their single chick at a lower rate than males raising two chicks and, thus, seem now to adjust their effort to brood size (Figure 5).

Additionally, we can also hypothesize that there are intrinsic quality differences between pairs that rear one versus two chicks (Clifford & Anderson, 2001; Gill & Hatch, 2002; Moe et al., 2002). The quality of females that hatch only one egg may be such that they are unable to feed at a higher frequency. This is supported by the fact that whereas 1-chick females feed their chick at a lower frequency than 2-chick females, they did not attend the nest more. This second hypothesis assumes that it is the characteristics of females of 1-chick pairs that lead to the hatching failure of the second egg. In many species, hatching success or egg composition has been shown to depend upon maternal phenotype. For instance, in spotless starling (*Sturnus unicolor*) female homozygosity affects hatchability, whereas male homozygosity does not (Cordero et al., 2004). Immune-challenged barn swallows (*Hirundo rustica*) and carotenoid-fed lesser black-backed gulls (*Larus fuscus*) produce eggs with smaller concentrations of carotenoids, a compound that is critical to embryonic development (Saino et al., 1999; Blount et al., 2000). In kittiwakes, causes of hatching failure are poorly understood. It has been shown however, that hatching success is higher when parents are food-supplemented (Gill & Hatch, 2002), and that egg composition in antibodies and androgen may depend upon female phenotype (Gasparini et al., 2002; 2007). We may, thus, expect that, in kittiwakes, low quality females lay unviable eggs more often.

Brood reduction

Our results show that when the rate of brood reduction is low (i.e., in 1999), neither males nor females fed their chicks at a lower rate than parents raising two chicks. A baseline level of brood reduction, therefore, does not seem to be due to low food delivery. In blue-footed boobies, a baseline level of aggression is expressed even when food is abundant (Drummond, 2001b). Brood reduction in 1999 may also not be due to siblicide but mainly to predation or chick falling out of the nest. In years when brood reduction rate is higher (i.e., in 2000 and 2001), before brood reduction, females of brood-reduction group fed their chick at a lower frequency (Figure 1) and delivered a lower amount of food to A-chick than females of 2-chick group (Figure 2). Furthermore, chick aggression was found to be correlated to the food amount delivered to A-chicks by females (Figure 3). These results support the idea that a part of brood reductions resulted from female low

food delivery causing siblicide, although we lack records of mortality cause. In kittiwakes, as in many other species (review in Drummond, 2001a), food shortage has been shown to increase chick aggression and siblicide (Braun & Hunt, 1983; Irons, 1992; White et al., 2010). Game theory models predict that partial compensation for a mate's reduced parental effort must occur to maintain a stable evolutionary strategy of biparental care (Houston & Davies, 1985; McNamara et al., 1999). Contrarily, we found that brood-reduction males did not increase their parental effort in response to female low food delivery. This suggests that males may be unable or unwilling to increase their parental effort. Two hypotheses may explain the low female feeding delivery.

First, low quality females may be unable to feed their chicks at a sufficient rate not to trigger brood reduction. The first part of chick rearing seems more energetically demanding for females than for males (Golet et al., 1998; Fyhn et al., 2001; Moe et al., 2002; Jodice et al., 2006) and individual quality may, thus, have more influence on female food delivery than on male food delivery. Several hypotheses have been suggested to explain why females should lay a maximum number of eggs, even though they could lose a chick. The main hypothesis suggests that, in fluctuating environment, brood reduction provides a mechanism that adjusts brood size to food resources during the nestling period ('resource tracking' hypothesis; Lack, 1947, 1954; Temme & Charnov, 1987). Many studies in birds have shown that growth and mortality of the smaller offspring is contingent upon environmental condition (e.g., Magrath, 1989; Forbes et al., 2001; Shawkey et al., 2004). Similarly, observations of kittiwakes showed higher level of chick aggression and siblicide in years of food shortages (Braun & Hunt, 1983; Irons, 1992). A second hypothesis suggests that marginal offspring are valuable as potential substitutes for defective members of the clutch ('insurance hypothesis'; Dorward, 1962; Forbes, 1990; Forbes et al., 2002; Townsend & Anderson, 2007). We found a high rate of hatching failure, ranging from 18 to 26%. Kittiwakes of any quality may, thus, adaptively produce two eggs as an insurance against the high probability of egg loss.

The second hypothesis, that may be proposed to explain why brood-reduction females delivered less food to their chicks than 2-chick females, suggests that their feeding effort is restrained and not constrained. Just after brood reduction females fed their remaining chick at the same rate as

2-chick females and attended the nest as often. This period seems still energetically demanding for females, (Moe et al., 2002), which suggests that their low food delivery before brood reduction may not be due to their inability to feed two small chicks but it may be adaptive. Life history theory predicts that, in iteroparous species, parental investment in current reproduction should be balanced by the costs in terms of residual reproductive value (Stearns, 1992). Consequently, if the current reproduction is not as valuable as the next reproductions, individuals may restrict their parental effort to maximise their residual reproductive value. For instance, females mated with incompatible or low quality males may reduce their feeding effort and, thus, save energy for next reproductions. Many studies have shown that females continuously evaluate their mate's quality and modify their breeding decision accordingly (e.g., Burley, 1988; Cunningham & Russell, 2000; Safran et al., 2005; Torres & Velando, 2005; Velando et al., 2006). Additionally, medium quality females that could not be able to take care of two old chicks may also adaptively restrict their effort during the early part of chick rearing. Those females would invest in the quality of their remaining chick rather than in a high number of offspring. Brood reduction may, thus, provide a mechanism that adjusts brood size to parental chick-rearing capacity, when the estimation of mate quality or of its own quality is uncertain at the beginning of the breeding period (Amundsen, 1993). The role of parents in the siblicidal behaviour of their chicks is poorly understood (Drummond, 2001a). In most species, parents generally give every appearance of being indifferent to even conspicuous violence among their nestlings (Mock & Forbes, 1992; Drummond, 1993) and chicks were thought to exert most of the control of parental food distribution. However, in some species, females take an active role in the distribution of food by for instance selectively feeding first-hatched chicks when food is scarce (Krebs & Magrath, 2000; Ploger & Medeiros, 2004; Budden & Beissinger, 2009; see review in Lessells, 2002). This inequality in chick feeding increases the advantage of A-chick in broodmate competition. Our study may suggest that, in kittiwakes, females use another strategy to promote brood reduction. They may adaptively decrease their food delivery to A-chick, which may enhance its aggressiveness and cause brood reduction. Congruently, food-supplemented parents have been shown to feed A-chicks, but not B-chicks, at a higher rate than control parents, which reduces the occurrence of sibling aggression and brood reduction (White et al., 2010). After brood reduction, we found that brood-reduction females fed

their single chick at the same rate as females raising two chicks (Figures 1, 2 and 4). After a starvation period inducing brood reduction, females would, thus, help their remaining chick to catch up growth and enhance their chick's phenotypic quality. This hypothesis is supported by the fact that when parents did not under-feed their chicks before brood reduction (i.e., 1999), they fed their single chick at a lower rate than parents raising two chicks after brood-reduction. This may suggest that, in such a year, the surviving chick does not need to catch up growth and parents can lower their effort. Data on chick growth would be necessary to test this hypothesis.

Our results lead us to propose several potential mechanisms to explain clutch and brood reduction in kittiwakes. Only experiments, such as altering male and/or female condition, may allow one to determine the relative weight of these hypothetical mechanisms in driving the adaptive functions of clutch and brood reduction and to identify which sex promotes family reduction in that species.

Acknowledgements

We are grateful to J. Guillaumin, F. Martayan and V. Nepoux for their help in field work and data collection and to Bretagne Vivante-SEPNB for providing access to the Réserve Naturelle du Cap-Sizun. The manuscript benefited greatly from the comments of D.W. Mock and S. Forbes. This project benefited from the scientific support of the French National Center of Scientific Research (CNRS) in the form of CNRS PICS grant no. 2410 to É.D. and R.H.W. and as part of the GDR CNRS 2155 Behavioural Ecology. S.L. was supported by the French Polar Institute Paul-Emile Victor (IPEV). The present study complies with the current laws of France.

References

- Altmann, J. (1974). Observational study of behavior: sampling methods. — *Behaviour* 49: 227-267.
- Amundsen, T. (1993). On the evolution of differential parental investment: hatching asynchrony, sex ratio, and egg size variation in birds. — PhD thesis, University of Oslo, Oslo.
- Beamonte-Barrientos, R., Velando, A., Drummond, H. & Torres, R. (2010). Senescence of maternal effects: aging influences egg quality and rearing capacities of a long-lived bird. — *Am. Nat.* 175: 469-480.
- Bennett, P.M. & Owens, I.P.F. (2002). Evolutionary ecology of birds: life histories, mating systems and extinction. — Oxford University Press, Oxford.
- Blount, J.D., Surai, P.F., Nager, R.G., Houston, D.C., Møller, A.P., Trewby, M.L. & Kennedy, M.W. (2002). Carotenoids and egg quality in the lesser black-backed gull *Larus fuscus*: a supplemental feeding study of maternal effects. — *Proc. R. Soc. Lond. B.* 269: 29-36.

- Braun, B.M. & Hunt, G.L. (1983). Brood reduction in black-legged kittiwakes. — *Auk* 100: 469-476.
- Budden, A.E. & Beissinger, S.R. (2009). Resource allocation varies with parental sex and brood size in the asynchronously hatching green-rumped parrotlet (*Forpus passerinus*). — *Behav. Ecol. Sociobiol.* 63: 637-647.
- Burley, N. (1988). The differential-allocation hypothesis — an experimental test. — *Am. Nat.* 132: 611-628.
- Cadiou, B. (1993). L'accession à la reproduction: un processus social d'ontogénèse. Cas de la mouette tridactyle (*Rissa tridactyla*). — PhD thesis, Université de Rennes.
- Carere, C. & Alleva, E. (1998). Sex differences in parental care in the common swift (*Apus apus*): effect of brood size and nestling age. — *Can. J. Zool.* 76: 1382-1387.
- Clifford, L.D. & Anderson, D.J. (2001). Food limitation explains most clutch size variation in the Nazca booby. — *J. Anim. Ecol.* 70: 539-545.
- Cordero, P.J., Aparico, J.M. & Veiga, J.P. (2004). Parental genetic characteristics and hatching success in the spotless starling, *Sturnus unicolor*. — *Anim. Behav.* 67: 637-642.
- Coulson, J.C. (1966). The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. — *J. Anim. Ecol.* 35: 269-279.
- 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.
- Cunningham, E.J.A. & Russell, A.F. (2000). Egg investment is influenced by male attractiveness in the mallard. — *Nature* 404: 74-77.
- Dawson, R.D. & Bortolotti, G.R. (2003). Parental effort of American kestrels: the role of variation in brood size. — *Can. J. Zool.* 81: 852-860.
- Dickens, M. & Hartley, I.R. (2007). Differences in parental food allocation rules: evidence for sexual conflict in the blue tit? — *Behav. Ecol.* 18: 674-679.
- Dorward, D.F. (1962). Comparative biology of the white booby and the brown booby *Sula* spp. at Ascension. — *Ibis* 103b: 174-200.
- Drummond, H. (1993). Have avian parents lost control of offspring aggression? — *Ethologia* 3: 187-198.
- Drummond, H. (2001a). The control and function of agonism in avian broodmates. — *Adv. Stud. Behav.* 30: 261-301.
- Drummond, H. (2001b). A reevaluation of the role of food in broodmate aggression. — *Anim. Behav.* 61: 517-526.
- Forbes, L.S. (1990). Insurance offspring and the evolution of avian clutch size. — *J. Theor. Biol.* 147: 345-359.
- Forbes, S., Glassey, B., Thornton, S. & Earle, L. (2001). The secondary adjustment of clutch size in red-winged blackbirds (*Agelaius phoeniceus*). — *Behav. Ecol. Sociobiol.* 20: 37-44.
- Forbes, S., Grosshans, R. & Glassey, B. (2002). Multiple incentives for parental optimism and brood reduction in blackbirds. — *Ecology* 83: 2529-2541.
- Fyhn, M., Gabrielsen, G.W., Nordoy, E.S., Moe, B., Langseth, I. & Bech, C. (2001). Individual variation in field metabolic rate of kittiwakes (*Rissa tridactyla*) during the chick-rearing period. — *Physiol. Biochem. Zool.* 74: 343-355.
- Gasparini, J., Boulonier, T., Gill, V.A., Gil, D., Hatch, S.A. & Roulin, A. (2007). Food availability affects the maternal transfer of androgens and antibodies into eggs of a colonial seabird. — *J. Evol. Biol.* 20: 874-880.

- Gasparini, J., McCoy, K.D., Tveraa, T. & Boulinier, T. (2002). Related concentrations of specific immunoglobulins against the Lyme disease agent *Borrelia burgdorferi* sensu lato in eggs, young and adults of the kittiwake (*Rissa tridactyla*). — *Ecol. Lett.* 5: 519-524.
- Gill, V.A. & Hatch, S.A. (2002). Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding. — *J. Avian Biol.* 33: 113-126.
- Golet, G.H., Irons, D.B. & Estes, J.A. (1998). Survival costs of chick rearing in black-legged kittiwakes. — *J. Anim. Ecol.* 67: 827-841.
- González-Solís, J., Croxall, J.P. & Wood, A.G. (2000). Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. — *Oikos* 90: 390-398.
- Groothuis, T.G.G., Muller, W., von Engelhardt, N., Carere, C. & Eising, C. (2005). Maternal hormones as a tool to adjust offspring phenotype in avian species. — *Neurosci. Biobehav. Rev.* 29: 329-352.
- Hamann, J., Andrews, B. & Cooke, F. (1986). The role of follicular atresia in inter-seasonal and intra-seasonal clutch size variation in Lesser snow geese (*Anser caerulescens caerulescens*). — *J. Anim. Ecol.* 55: 481-489.
- Helfenstein, F., Tirard, C., Danchin, E. & Wagner, R.H. (2004). Low frequency of extra-pair paternity and high frequency of adoption in Black-legged Kittiwakes. — *Condor* 106: 149-155.
- Helfenstein, F., Wagner, R.H. & Danchin, E. (2003). Sexual conflict over sperm ejection in monogamous pairs of kittiwakes *Rissa tridactyla*. — *Behav. Ecol. Sociobiol.* 54: 370-376.
- Houston, A.I. & Davies, N.B. (1985). The evolution of cooperation and life history in the dunnoek *Prunella modularis*. — In: *Behavioural ecology* (Sybil, R.M. & Smith, R.H., eds). Blackwell Scientific, Oxford, p. 471-487.
- Irons, D.B. (1992). Aspects of foraging behavior and reproductive biology of the black-legged kittiwake. — PhD thesis, University of California, Irvine, CA.
- Jacobsen, K.O., Erikstad, K.E. & Saether, 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., Suryan, R.M., Irons, D.B., Turco, K.R., Brown, E.D., Thedinga, J.F. & Visser, G.H. (2006). Increased energy expenditure by a seabird in response to higher food abundance. — *Mar. Ecol. Prog. Ser.* 306: 283-293.
- Johnsen, I., Erikstad, K.E. & Saether, B.E. (1994). Regulation of parental investment in a long-lived seabird, the puffin *Fratercula artica*. — *Oikos* 71: 273-278.
- Kloskowski, J. (2003). Brood reduction in the red-necked grebe *Podiceps grisegena*. — *Ibis* 145: 233-243.
- Kozlowski, J. & Stearns, S.C. (1989). Hypotheses for the production of excess zygotes — models of bet-hedging and selective abortion. — *Evolution* 43: 1369-1377.
- Krebs, E.A. & Magrath, R.D. (2000). Food allocation in crimson rosella broods: parents differ in their responses to chick hunger. — *Anim. Behav.* 59: 739-751.
- 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.
- Lack, D. (1968). *Ecological adaptations for breeding in birds*. — Methuen, London.
- Lessells, C.M. (2002). Parentally biased favouritism: why should parents specialize in caring for different offspring? — *Phil. Trans. Roy. Soc. Lond. B: Biol.* 357: 381-403.

- Lessells, C.M. (2006). The evolutionary outcome of sexual conflict. — *Phil. Trans. Roy. Soc. Lond. B: Biol.* 361: 301-317.
- Lewis, S., Benvenuti, S., Dall'antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S. & Hamer, K.C. (2002). Sex-specific foraging behaviour in a monomorphic seabird. — *Proc. Roy. Soc. Lond. B: Biol.* 269: 1687-1693.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D. & Schabenberger, O. (2006). SAS for mixed models. — SAS Institute, Cary, NC.
- Lobato, E., Moreno, J., Merino, S., Sanz, J.J., Arriero, E., Morales, J., Tomas, G. & La Puente, J.M.D. (2006). Maternal clutch reduction in the pied flycatcher *Ficedula hypoleuca*: an undescribed clutch size adjustment mechanism. — *J. Avian Biol.* 37: 637-641.
- Lombardo, M.P. (1991). Sexual differences in parental effort during the nestling period in tree swallows (*Tachycineta bicolor*). — *Auk* 108: 393-404.
- Magrath, R.D. (1989). Hatching asynchrony and reproductive success in the blackbird. — *Nature* 339: 536-538.
- Magrath, R.D. (1990). Hatching asynchrony in altricial birds. — *Biol. Rev. Camb. Philos. Soc.* 65: 587-622.
- Massaro, M., Chardine, J.W., Jones, I.L. & Robertson, G.J. (2000). Delayed capelin (*Mallotus villosus*) availability influences predatory behaviour of large gulls on black-legged kittiwakes (*Rissa tridactyla*), causing a reduction in kittiwake breeding success. — *Can. J. Zool.* 78: 1588-1596.
- Mauck, R.A. & Grubb, T.C. (1995). Petrel parents shunt all experimentally increased reproductive costs to their offspring. — *Anim. Behav.* 49: 999-1008.
- McNamara, J.M., Gasson, C.E. & Houston, A.I. (1999). Incorporating rules for responding into evolutionary games. — *Nature* 401: 368-371.
- Mock, D.W. & Forbes, L.S. (1992). Parent-offspring conflict: a case of arrested development? — *Trends Ecol. Evol.* 7: 409-413.
- Mock, D.W. & Forbes, L.S. (1995). The evolution of parental optimism. — *Trends Ecol. Evol.* 10: 130-134.
- Mock, D.W. & Parker, G.A. (1997). The evolution of sibling rivalry. — Oxford University Press, Oxford.
- Mock, D.W. & Parker, G.A. (1998). Siblicide, family conflict and the evolutionary limits of selfishness. — *Anim. Behav.* 56: 1-10.
- Moe, B., Langseth, I., Fyhn, M., Gabrielsen, G.W. & Bech, C. (2002). Changes in body condition in breeding kittiwakes *Rissa tridactyla*. — *J. Avian Biol.* 33: 225-234.
- Mulard, H., Danchin, E., Talbot, S.L., Ramey, A.M., Hatch, S.A., White, J.F., Helfenstein, F. & Wagner, R.H. (2009). Evidence that pairing with genetically similar mates is maladaptive in a monogamous bird. — *BMC Evol. Biol.* 9: 147.
- Ploger, B.J. & Medeiros, M.J. (2004). Unequal food distribution among great egret *Ardea alba* nestlings: parental choice or sibling aggression? — *J. Avian Biol.* 35: 399-404.
- Quillfeldt, P., Masello, J.F. & Hamer, K.C. (2004). Sex differences in provisioning rules and honest signalling of need in Manx shearwaters, *Puffinus puffinus*. — *Anim. Behav.* 68: 613-620.
- Safran, R.J., Neuman, C.R., McGraw, K.J. & Lovette, I.J. (2005). Dynamic paternity allocation as a function of male plumage color in barn swallows. — *Science* 309: 2210-2212.
- Saino, N., Stradi, R., Ninni, P., Pini, E. & Møller, A.P. (1999). Carotenoid plasma concentration, immune profile, and plumage ornamentation of male barn swallows (*Hirundo rustica*). — *Am. Nat.* 154: 441-448.

- Salamolard, M. & Weimerskirch, H. (1993). Relationship between foraging effort and energy requirement throughout the breeding-season in the wandering albatross. — *Funct. Ecol.* 7: 643-652.
- Sanz, J.J., Kranenbarg, S. & Tinbergen, J.M. (2000). Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). — *J. Anim. Ecol.* 69: 74-84.
- Shawkey, M.D., Bowman, R., Woolfenden, G.E. (2004). Why is brood-reduction in Florida scrub-jays higher in suburban than in wildland habitats? — *Can. J. Zool.* 82: 1427-1435.
- St. Clair, C.C., Waas, J.R., St. Clair, R.C. & Boag, P.T. (1995). Unfit mothers — maternal infanticide in royal penguins. — *Anim. Behav.* 50: 1177-1185.
- Stearns, S.C. (1992). *The evolution of life histories*. — Oxford University Press, Oxford.
- Stoleson, S.H. & Beissinger, S.R. (1997). Hatching asynchrony, brood reduction, and food limitation in a neotropical parrot. — *Ecol. Monogr.* 67: 131-154.
- Tanzev, A., Parisot, M., Chastel, O. & Leboucher, G. (2008). Does maternal social hierarchy affect yolk testosterone deposition in domesticated canaries? — *Anim. Behav.* 75: 929-934.
- Temme, D.H. & Charnov, E.L. (1987). Brood size adjustment in birds: economical tracking in a temporally varying environment. — *J. Theor. Biol.* 126: 137-147.
- Torres, R. & Velando, A. (2005). Male preference for female foot colour in the socially monogamous blue-footed booby, *Sula nebouxi*. — *Anim. Behav.* 69: 59-65.
- Townsend, H.M. & Anderson, D.J. (2007). Production of insurance eggs in Nazca boobies: costs, benefits, and variable parental quality. — *Behav. Ecol.* 18: 841-848.
- Trivers, R.L. (1972). Parental investment and sexual selection. — In: *Sexual selection and the descent of man* (Campbell, B.G., ed.). Aldine, Chicago, IL, p. 136-179.
- Urrutia, L.P. & Drummond, H. (1990). Brood reduction and parental infanticide in Heermann's gull. — *Auk* 107: 772-774.
- Velando, A. & Alonso-Alvarez, C. (2003). Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. — *J. Anim. Ecol.* 72: 846-856.
- Velando, A., Beamonte-Barrientos, R. & Torres, R. (2006). Pigment-based skin colour in the blue-footed booby: an honest signal of current condition used by females to adjust reproductive investment. — *Oecologia* 149: 535-542.
- 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.
- White, J., Wagner, R.H., Helfenstein, F., Hatch, S.A., Mulard, H., Naves, L.C. & Danchin, E. (2008). Multiple deleterious effects of experimentally aged sperm in a monogamous bird. — *Proc. Natl. Acad. Sci. USA* 105: 13947-13952.
- Wiebe, K.L. & Bortolotti, G.R. (1994). Food-supply and hatching spans of birds — energy constraints or facultative manipulation. — *Ecology* 75: 813-823.
- Zielinski, P. (2002). Brood reduction and parental infanticide: are the white stork *Ciconia ciconia* and the black stork *C. nigra* exceptional? — *Acta Ornithol.* 37: 113-119.
-