THE IMPORTANCE OF BROOD SEX RATIO ON SURVIVAL OF HERRING GULL (LARUS ARGENTATUS) CHICKS IN YEARS WITH FOOD SCARCITY

BETYDNINGEN AV KULLETS KJØNNSRATIO FOR OVERLEVELSEN AV UNGER HOS GRÅMÅKE I ÅR MED BEGRENSET MATTILGANG

ELISABETH RESSEM KVIVESEN

Norwegian University of Life Sciences
Department of Ecology and Natural Resource Management
Master Thesis 30 credits 2009

Forord

Denne masteroppgaven har vært gjennomført i samarbeid med Norsk institutt for naturforskning (NINA) i Tromsø. Undersøkelsen er del av et nasjonalt forskningsprogram på sjøfugl (SEAPOP). SEAPOP har som mål å innhente og opprettholde kunnskap om norske sjøfuglbestander for å forbedre forvaltningen av marine områder. Hornøya, hvor feltarbeidet ble utført, er en av nøkkellokalitetene for dette programmet.

Jeg vil takke min hovedveileder seniorforsker Kjell Einar Erikstad for muligheten til å skrive en masteroppgave som kan bidra til forskning på sjøfugl, samt for uvurderlig veiledning med oppgaven, i tillegg til gode råd og oppmuntring underveis.

Dataene som er brukt i denne oppgaven er innhentet av meg selv i 2008, mens data fra 2006 og 2007 er innhentet av Trond S. Jenssen. Jeg vil derfor takke han for denne innsatsen, samt god opplæring av feltarbeid.

Jeg vil også takke mine tilleggsveiledere Svein Dale ved UMB for verdifulle innspill, og Truls Moum ved Høgskolen i Bodø for analyse av blodprøver, i tillegg vil jeg også takke Tone Kristin Reiertsen for gode innspill mot slutten av oppgaveskrivingen.

Til slutt vil jeg takke min familie og mine venner for all støtte underveis (både økonomisk og moralsk), og ikke minst min kjære samboer fordi han har holdt ut med meg underveis og hjulpet meg både i gode og mindre gode dager.

Vardø, 1.juni 2009

Elisabeth Kvivesen

Abstract

In species with sexual size dimorphism the larger sex is expected to be more vulnerable during adverse conditions because of its higher energy demand (the “energy demand” hypothesis). This could lead to a skewed sex-ratio towards the cheaper sex when conditions are unfavorable. In species with more than one offspring it is also expected that the larger sex could have a competitive advantage over the smaller sex (the “competitive advantage” hypothesis). Many species of bird are able to manipulate the sex of their offspring according to what is most favorable according to environmentally conditions.

During three bad breeding seasons the survival of herring gull chicks until 15 days after hatching was investigated in relation to which brood sex ratio group they grew up in (all-male, mixed or all-female). All-female broods had a significant higher survival compared to all other brood sex ratio groups. The results gave support to the “energy demand” hypothesis, but not to the “competitive advantage” hypothesis. A possible competitive advantage of males in mixed broods could have been outweighed by their higher energy demand during such poor breeding seasons, which also negatively affected the whole brood.

The sex ratio at hatching was male-biased (0.57 male offspring) in contrast to other studies during poor conditions. A possible explanation for this is that females in poor body condition producing an excess of female offspring are more vulnerable to egg predation.

Because of the higher survival of all female broods in all three years the sex ratio 15 days after hatching was slightly, but not significantly female-biased (0.45 male offspring). This could lead to an overproduction of females at the population level if the breeding seasons are poor over several years. An overproduction of the more expensive sex would in this situation be more beneficial, because the chances of finding a mate for a male would be higher than for females in a female-biased population.

Sammendrag

Hos arter med kjønnsdimorfisme er det forventet at det største kjønnet er mer sårbar under ugunstige forhold på grunn av sitt høyere energikrav (”energy demand” hypotesen). Dette kan føre til en skjev kjønnsratio i favør av det billigste kjønnet når forholdene ikke er optimale. Hos arter med flere avkom per kull er det også forventet at det største kjønnet kan ha en konkurransefordel over det minste kjønnet (”competitive advantage” hypotesen). Mange fuglearter er i stand til å manipulere kjønnet på avkom etter hva som er mest fordelaktig under gitte miljøbetingelser.

I løpet av tre dårlige hekkesesonger ble overlevelsen av gråmåkeunger frem til 15 dagers undersøkt i forhold til kullets kjønnsratiogruppe (rene hannkull, miksa kull og rene hunnkull). Rene hunnkull hadde en signifikant høyere overlevelse enn de andre kjønnsratiogruppene. Resultatene ga støtte ”energy demand” hypotesen, men ikke til ”competitive advantage ” hypotesen. En eventuell konkurransefordel hos hanner kunne likevel ha blitt overskygget av det høyere energikravet under så dårlige forhold, noe som også ville påvirket hele kullets overlevelse.

Kjønnsratioen ved klekking var marginalt forskjøvet mot hanner (0.57 hanner) i kontrast til andre studier under dårlige hekkeforhold. En mulig forklaring på dette er at hunner i dårlig kondisjon som man antar produserer et overskudd av hunner også var mer utsatt for eggpredasjon.

På grunn av den høyere overlevelsen i rene hunnkull i alle sesongene var kjønnsratioen 15 dager etter klekking noe, men ikke signifikant, forskjøvet mot hunner (0.45 hanner). Dette kan føre til en overproduksjon på populasjonsnivå hvis dårlige hekkeforhold vedvarer over flere år. I en slik situasjon vil en høyere investering av det kostbare kjønnet være gunstig på grunn av at sjansen for å finne en make vil være større for en hann i en bestand med overtall av hunner.

Introduction

Sex ratio theory is an important part of the population biology discipline (Clutton-Brock 1986; Donald 2007). Reproduction is an expensive investment (Monaghan *et al.* 1998; Pugesek & Diem 1990), so parents have to balance their reproductive investment between one season and their own survival, and the possibilities of future reproduction (Erikstad *et al.* 1998; Pugesek 1990). Traditionally the sex ratio in a population is expected to always fluctuate around 50:50, because the natural selection favors production of the rarest sex (Fisher 1930). In species with sexual size dimorphism it is expected that one of the sexes is more expensive to raise (Cameron-MacMillian *et al*. 2007), and it has been suggested that mothers in poor condition should invest in the cheapest sex, while mothers in good condition should invest in the most expensive sex (Trivers & Willard 1973).

It is also expected that the largest sex is more vulnerable during adverse conditions because of its higher energy demand. This has been documented in relation to food shortage (Clutton-Brock *et al.*1985; Røskaft & Slagsvold 1985), low egg quality (Nager *et al.* (1999) and increased maternal stress hormones (Love *et al.* 2005). This is also known as the "energy demand" hypothesis. In species with more than one offspring, a brood consisting of the largest sex will have a higher energy demand than a brood consisting of the smallest sex (Müller *et al.* 2005). It has also been suggested that the chance of brood reduction will increase with an increased number of the larger sex in a brood (Dijkstra *et al.* 1998), and in some species it has been reported that the largest sex has better survival than the smaller sex in mixed broods (Arroyo 2002; Fargallo *et al.* 2006). An explanation for this is that the largest sex could have a competitive advantage over their smaller siblings because of its bigger size, and this is referred to as the "competitive advantage" hypothesis. It has been shown that parents can manipulate the sex of the offspring based on what gives the largest reproductive success under different resource situations (Dijkstra *et al*. 1990; Komdeur 1996; Torres & Drummond 1999) or their own body condition (Nager *et al.* 1999, Kalmbach *et al.* 2001). Both brood sex ratio and the degree of intra brood competition can therefore to a large extent be controlled by the parents, by producing broods of different sex ratio compositions or by placing offspring sex to a certain position in the hatching sequence (Badyaev *et al*. 2002).

If, however, food conditions during the breeding season are unpredictable, it will be more difficult to predict the optimal brood sex ratio, as suggested by Griffiths (1992). Even parents in good condition can have trouble raising offspring if the food availability during the breeding season is low, especially if their brood sex ratio is skewed towards the largest sex. It could in this situation be favorable to have adaptive mechanisms enhancing brood reduction in order to reduce the total energy demand of the brood during poor conditions, and thus giving the remaining offspring a higher probability of survival (O'Connor 1978; Lack 1954). Asynchronous hatching is suggested to be such a mechanism, because it creates a size hierarchy within the brood, giving the larger offspring a competitive advantage over the smaller offspring (Lack 1954). Other possibilities for parents to create a size hierarchy among offspring could be to produce eggs of different size (Blanco *et al.* 2003) or nutritional content (Royle *et al.* 1999), or feed the offspring selectively (O'Connor 1978).

Any competitive advantage gained by being the largest sex can also depend on their position in the hatching sequence (Bradbury & Griffiths 1999; Torres & Drummond 1997). If the first hatched chick also is of the larger sex it could have an even bigger advantage over the smaller siblings. On the other hand, if the largest sex is positioned last in the hatching sequence it could, however, have the opposite effect, and the smallest sex could better compete with its larger siblings for food (Hébert & Barclay 1986). However, such an effect also seems to depend on food conditions. In periods of good food condition it can pay off to choose a brood that gives the largest possible survival for the entire brood with as little competitive difference between offspring as possible. This can be done by positioning the smallest sex first in the sequence (Kim & Monaghan 2006) or by more synchronous hatching (Davis & Quinn 1997; Hillström *et al*. 2000), while under poor conditions it would be better to have the brood reduction happen as early as possible (Lack 1954).

In the present study the survival of herring gull chicks were examined in relation to the sex ratio of the brood they grew up in. Herring gulls are sexually dimorphic, where the male is about 20 % larger than the females (Malling-Olsen & Larsson 2003). They normally lay a clutch of 3 eggs that hatches asynchronously (Haftorn 1971). The third egg is usually smaller than the first and second egg and also often hatches 1-2 days later than their siblings, creating a size hierarchy where the smallest young is at a disadvantage compared to the others (Davis & Quinn 1997; Hérbert & Barclay 1986). Herring gulls do not feed their offspring separately, but regurgitate the food on the ground (Davis & Quinn 1997; Hillström *et al*. 2000). This may prevent the parents from selectively feeding the chicks and opens for sibling competition, where the largest chick gets more food. When parents do not discriminate the chicks at feeding, as Hillström *et al*. (2000) observated, all chicks can get just enough food to survive long enough to reduce the survival chance for the entire brood.

The present study population experienced very low food availability during the three years of this study. This gave a good opportunity to sort out some of the mechanisms explaining the differential survival of male and female offspring during poor conditions. If males have a lower survival rate because of their higher energy demand as suggested by the “energy demand” hypothesis, one could expect that a brood with more male offspring will have a lower survival rate than broods with many female offspring. All-male broods will then be expected to have a lower survival rate than all-female broods. In mixed broods, however, males can have a competitive advantage by being the larger sex, thus if there is in fact a lower survival rate in all-male broods this might be weighed up for by males having a higher rate of survival in mixed broods. During extra poor conditions, however, one male could be enough to increase the energy demand for the entire brood beyond of what the parents can provide, especially when one chick is not able to monopolize the food totally. In this situation it is thereby expected that parents producing the least energy-demanding brood, all-females, will be most successful.

Methods

A breeding population of herring gulls was studied at Hornøya (70°23´N, 31°09´E), Norway during three breeding season (2006-2008). Hornøya is a 0,7 km^2 island located in the southern part of the Barents Sea, and is the breeding site for many seabirds, including a large colony of herring gulls. A total number of 110 (2006), 118 (2007) and 110 (2008) herring gull nests were registered at the beginning of the nesting season (May) every year. Due to a very high predation rate of eggs, only a total of 22, 25 and 16 nests for 2006, 2007 and 2008 respectively, could be used in the analysis. Every nest was marked with a metal stick with an individual nest number. The eggs were measured and marked with an individual number. If possible the laying sequence was registered. The nests were then checked every 2-3 days, and at the end of the brooding period they were checked once a day to determine the hatching date of the chicks. Hatching chicks with visible beaks was marked with a colored felt pen on the beak to be able to connect the chick to its egg number after hatching. Every chick was marked with a band where nest number and chick number were printed on. If possible hatching sequence was also registered. The nests were then checked every 3-5 days for about 20 days to register missing or dead chicks. A chick was assumed dead if not found in 3 visits to the nest in a row. The chicks were weighed at the day of hatching. The chicks were weighed to the nearest gram (g) with a pesola spring scale of 100 g. At hatching a small blood sample (5-10 µl) was taken to determine sex. The blood sample was taken from the foot-vein with a needle and a 10 µl pipette, and stored in small tubes containing 0.5ml Queens lysis buffer for later analyzes.

Sex-determination and DNA analyses

The DNA analysis method was done as described by Griffiths *et al.* (1998). For this method the PCR-primer (P2 and P8) is used, which consequently amplifies a particular part of the gene, and gives an intron of different sizes for the CHD1-W and CHD1-Z genes.

Statistical analyses

Only nests where at least 2 chicks hatched, and the sex of all chicks in the brood was known, were included in the analysis. The total number of chicks used in the analysis was 46 in 2006, 45 in 2007 and 40 in 2008. The chicks were grouped according to the sex ratio of the broods ("brood sex ratio groups"): females, males or mixed broods.

To analyse the sex ratio at the brood level a generalized linear mixed model was used with the number of male offspring as the response variable and brood size (or number of chicks hatched) as the binominal denominator and a log link function. The survival of male and female offspring in a brood sex ratio group was analysed specifying a binominal error distribution and a log link. To account for clustering of data as a result of nest identity, we used nest identity as a random factor. In all analyses, we used a backward elimination (based on AIC values). All tests are 2-tailed and all analysis was carried out in SAS (2008).

Results

The egg laying date did not differ between years, but both clutch size, egg volume, hatching date, the hatching body mass of chicks and number of chicks survived per nest until 15 days was significantly different. The general trend was that 2007 was a somewhat better season having both larger eggs and larger hatching body mass of chicks compared to 2006 and 2008 (table 1).

***Table 1**: Annual variation in clutch size, egg volume, hatching date and hatching weight at Hornøya. Values with similar letters (A,B,C) are not significantly different. Differences between years are tested using an ANOVA.*

	Year			Statistics	
	2006	2007	2008	*F*	*P*
Laying date	11.2±0.3 (33)	12.6±1.0 (19)	13.0±1.3 (8)	1.78	0.1781
Clutch size	2.6±0.1 (54)A	2.7±0.1 (65)AB	2.8±0.1 (44)B	3.30	0.0394
Egg volume (cm^3)	89.0±1.0 (54)A	95.9±0.9 (65)B	89.9±1.1 (41)A	15.39	<.0001
Hatching date	40.3±0.4 (54)A	32.3±0.9 (65)B	40.3±1.2 (41)A	32.10	<.0001
Hatching weight (g)	63.6±0.9 (46)A	71.8±1.0 (45)B	68.2±1.6 (40)B	12.52	<.0001
No of chicks survived per nest	0.09±0.04(34)A	0.42±0.07(43)B	0.32±0.07(37)B	6.72	<0.003

Sex ratio at hatching

For broods where 2-3 chicks hatched, there was no significant difference in the frequency of brood sex ratio groups between years (χ^2= 3.70, *P*= 0.50, *df*=4, *n*=69). There was a trend, however, that there were less all-female broods in 2006 and 2008 (27.7 % and 9.1 %) than in 2007 (63.6 %) (table 2).

***Table 2**: The frequency of brood sex ratio groups produced for all three years.*

	2006	2007	2008
Males	40.00 (8)	30.00 (6)	30.00 (6)
Females	27.27 (3)	63.64 (7)	9.09 (1)
Mixed	34.21 (13)	39.47 (15)	26.32 (10)

The sex ratio at hatching was skewed towards males every year, though not significantly so (table 2). However, for all three years pooled the sex ratio was marginally significant different from 50:50 (0.57 in favor of males) (table 3).

***Table 3**: Sex ratios (proportion of male offspring) at hatching over three reproductive seasons at Hornøya. The statistical test (binominal test) shows the probability that sex ratio deviates from even (50:50) together with the 95% confidence limits.*

Year	Ratio	*n*	*Z*	*P*	*95 % CL*	
2006	0.61	54	1.63	0.10	0.49	0.72
2007	0.52	65	0.37	0.71	0.41	0.63
2008	0.59	44	1.21	0.23	0.46	0.72
Total	0.57	163	1.80	0.07	0.49	0.65

Survival of chicks

Overall there were no broods where 3 chicks survived until 15 days in any year. There were no significant differences in the survival of male and female offspring during the first 15 days after hatching (Wald χ^2= 2.41, P=0.12, df=1). However, there was a significant difference in survival of chicks when the data were grouped according to brood sex ratio groups (Wald χ^2=17.14, P=0.0007, df=3). For all three years chicks in the category female broods survived best (figure 1). There was also a significant difference in probability of survival between years (Wald χ^2= 10.74, P=0.0046, df=2) and this trend was apparent in all brood sex ratio groups (figure 1).

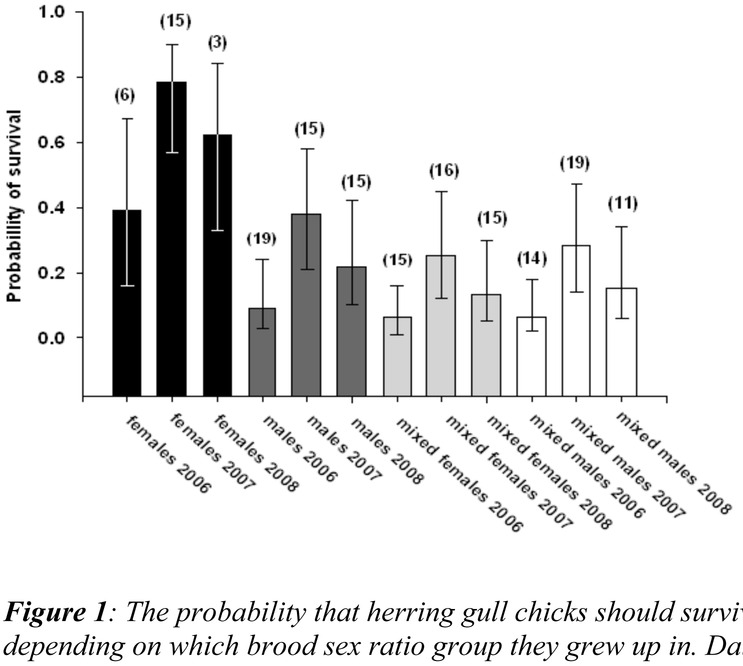

***Figure 1**: The probability that herring gull chicks should survive during 15 days after hatching depending on which brood sex ratio group they grew up in. Data for all three years (2006-2008).*

The odds ratio table for herring gull survival shows that the all-female broods had a much greater probability of survival (5 to 10 times higher) than the other family groups (table 4). The difference between years was smaller compared to the difference between groups.

***Table 4**: Odd ratio estimates with confidence limits for differences in survival of chicks in different brood sex ratio groups and between different years. Odds ratios are taken from a logistic model estimating chicks survival in relation to brood sex ratio group and year.*

	Estimate	95% confidence limits	
Females vs Males	5.845	1.835	18.617
Females vs Mixedf	10.616	3.063	36.791
Females vs Mixedm	9.211	2.732	31.059
Males vs Mixedf	1.816	0.613	5.380
Males vs Mixedm	1.576	0.543	4.570
Mixedf vs Mixedm	0.868	0.276	2.730
Year 2006 vs 2007	0.176	0.061	0.509
Year 2006 vs 2008	0.381	0.115	1.262
Year 2007 vs 2008	2.160	0.835	5.590

There was a significant positive correlation between hatching weight of chicks and their probability of survival (Wald χ^2=5.2, P=0.02), which was not sex-specific (Wald χ^2=0.73, P=0.39) (figure 2). This indicates that survival was more affected by body size than sex. There was also a significant difference in hatching weight between chicks within a brood (F=7.32, P=0.001, df=2). This was due to chick 3 in the hatching poition being lighter than it`s two older siblings (table 5), but again this differences was not related to sex. This may indicate that the last chick in the laying position are more likely to die first.

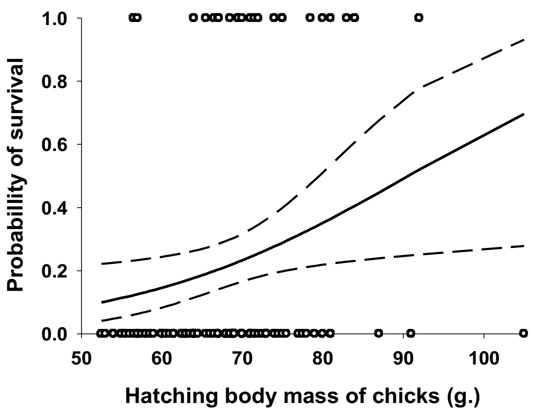

***Figure 2**: The probability that chicks should survive in relation to their body weight at hatching. Bold line shows the mean probability of survival and stippled lines shows the upper and lower 95% confidence limits. Open circles indicate the observed values of survival.*

***Table 5**: The hatching body weight of chicks in relation to their hatching order.*

Chick number	Hatching weight (mean)	*n*	*SE*
1	67.7	32	1.2
2	66.1	32	1.2
3	59.6	13	1.5

Sex ratio of 15 day old chicks

The sample size on 15 day old chicks was too low to calculate any statistical differences for each year separately. Thus all years were pooled to estimate the deviation from an even sex ratio. After 15 days the sex ratio was skewed towards female offspring but not significantly different from even (0.45, n=42) (Z=0.62, P=0.54, CL: 0.32-0.59), but this could also be an effect of the small sample size and low power of the analyses. Due to the higher survival of female offspring, the sex ratio for all years pooled shifted from a marginal surplus of males to a marginal surplus of females (0.57 - 0.45), but the sex ratio at hatching and after 15 days did not differ (Wald χ^2= 0.30, P=0.58, df=1).

Discussion

The probability of survival for all three years did not differ between sexes, but did differ between brood sex-ratio groups. This was caused by the higher probability of survival in all female broods. The sex-ratio was marginally male-biased at hatching (0.57 male offspring), while for 15 day old chicks it was slightly female biased (0.45 male offspring), but not different from even. The poorer survival in all male broods compared to all female broods gives support to the energy demand hypothesis. In mixed brood neither sex did have any advantage, probably due to the higher energy demand of males affected the rest of the brood too.

The general trend was that 2007 was a slightly better season than 2006 and 2008, both according to egg size and hatching weight of chicks, and the probability that chicks would live 15 days. The survival of 15 day old chicks at Hornøya was 11 %, 41 % and 20 % in 2006, 2007 and 2008 respectively, but compared to other gull studies none of the years can be characterized as "good". In a study of herring gulls over 3 years in an area with no apparent food-limits, the survival of 15 day old chicks were 59 %, 67 % and 49 % (Kadlec *et al.* 1969). In another study on herring gulls the survival of 10 day old chicks was 75 % (Hillström *et al.* 2000). This indicates that all of the 3 breeding seasons on Hornøya can be referred to as "bad".

Energy demand hypothesis and brood sex ratio groups

Overall there were no significant differences in survival between male and female offspring until 15 days after hatching in any year. There was, however, a significant difference between brood sex ratio groups, caused by the higher probability of survival in all-female broods compared to the other brood sex ratio groups. The higher survival of all-female broods supports the energy demand hypothesis, and is consistent with the results of other studies on survival between sex ratio groups (Black-headed gull *Larus ridibundus* in Müller *et al.* 2005; Lesser black-backed gulls *Larus fuscus* in Nager *et al.* 2000 and Chinstrap penguins *Pygoscelis antarctica* in Fargallo *et al.* 2006).

In mixed broods there were no differences in survival between male and female offspring, giving no evidence of male siblings having a competitive advantage over female siblings. This is consistent with a study on European kestrels *Falco tinniculus* during a season of low food abundance (both sexes had an equally low survival) (Laaksonen *et al.* 2004). This could be due to the importance of food abundance overriding the effects of any possible competitive advantage, as Laaksonen *et al.* (2004) suggested. A competitive advantage may also depend on a certain level of size dimorphism between chicks, as in chinstrap penguins, where male sibling had a competitive advantage over female siblings, but only if hatched first (Fargallo *et al.* 2006). The survival of chicks was, however, very good (76-100 %), and one cannot exclude the possibility that when the environmental conditions are under a certain threshold, the energy demand of the larger chick may override a possible size mediated competitive advantage.

Below the few other studies which have examined the survival of male and female chicks in different brood sex ratio groups, is reviewed (table X).

***Table X**: A review of studies which have examined the survival of chicks in different brood sex ratio groups under different environmental conditions. The chance of survival of each group is given as a range from 1-3, where 1 is most likely to survive and 3 is least.*

Condition (environmental, parental etc)	High food abundance	Natural intermediate conditions	Experimental lower parental condition	Lower food abundance	Natural poor Conditions
Reference/ Species	1/European kestrels	2 /Chinstrap penguins	3/Lesser black-backed gull	4/European kestrels	5/Herring gulls
Brood sex ratio groups					
All-females	Good	1 Good	1 Good	2 Poor***	1 Good
All-males	Good	3 Poor	3 Poor	1 Good	2 Poor
Mixed	Good	2 Good *	2 Good **	3 Poor	2 Poor

**Male chicks had a better survival than female chicks.*

***Male chicks had significantly lower weights than control chicks in mixed broods.*

****Females chicks had a lower haematrocrit level (an index of nutritional condition and health state).*

1. Laaksonen *et al.* 2004 (good season), 2. Fargallo *et al.* 2006, 3. Nager *et al.* 2000, 4. Laaksonen *et al.* 2004 (bad season), 5. Hornøya (three bad seasons).

Table X shows a gradient change of survival between brood sex ratio groups from good conditions on the left to very bad conditions on the right. When the breeding conditions are unfavourable, this negatively affects all-male broods (= all-female broods in kestrels, where females are the larger sex), while all-female broods do better. In mixed broods the trend is a gradient from equally good survival between sexes under very good conditions to equally bad survival under very poor conditions.

The only situation where males had a competitive advantage over female siblings (chinstrap penguins, table X) the survival of chicks was very good, in addition to a relative large age difference between the two chicks (1-4 days in hatching asynchrony) (Fargallo *et al*. 2006). The age difference between chick 1 and 2 in herring gulls is usually less than 1 day, and often they have a third sibling to compete with (Hébert & Barclay 1986). Herring gulls do not feed their chicks individually, which can make it more difficult for one chick to monopolize the food (Davis & Quinn 1997, Hillström *et al*. 2000). The size and age difference between chick 1 and 2 may not be large enough for one sibling to completely exclude another sibling from getting any food, and without any dominance hierarchy within the brood, siblings could spend unnecessary energy on sibling competition (Drummond *et al*. 1991). During very poor conditions as seen on Hornøya, the brood`s total energy demand could be too large for what the parents can provide, especially if the condition of parents is poor (Nager *et al*. 2000).

Maternal condition was not investigated at Hornøya, however this can still be of great importance for brood sex ratios. Trivers and Willard (1973) expected that females in poor conditions should invest in the cheapest sex, while mothers in good conditions would gain more fitness by investing in the more expensive sex. If parental condition was correlated with the quality of the season, there should have been an overproduction of the cheapest sex in all three years at Hornøya, as found in other studies (Nager *et al*. 1999; Kalmbach 2001; Torres & Drummond 1999). This was not the case at Hornøya, in fact there was a tendency that all-female broods was less common in the two poorest seasons. In addition there was a marginally skewed sex ratio of males at hatching. This could be due to differential food availability from the timing of egg production to the nestling periode, causing a production of a more expensive brood than what is possible to raise when food availability is poor. Fish offal could be such an unpredictable food source, and is dependent on the local fishery (Oro *et al.* 1996). However, both egg volumes were smaller and hatching dates later in 2006 and 2008, which indicates that the environmental condition during egg production was also poor in these years.

Another explanation could be that parents in poor condition choose not to reproduce to avoid risking own survival. Since reproduction is very costly the maternal condition should be above a certain threshold before attempting to breed (Erikstad *et al.* 1998). During very poor condition parents in poor condition could be the first to give up a breeding attempt, and only parents in relatively good condition remain to breed. According to Trivers and Willard (1973) these parents might rather skew the sex ratio of chicks towards males, giving a situation as observed at Hornøya. Conspecific predation is very common in herring gulls, and unexperienced /poor quality parents could be less able to protect eggs from predation (Bogdonova *et al*. 2007; Kadlec *et al.*1969), or need to spend more time foraging than protecting their nests (Bukacinska *et al.* 1996). Also Bogdonova *et al.* (2007) suggested that females are more susceptible to variation in the incubation environment than males when raised by young parents. This might explain why an expected female overproduction did not appear when only considering the sex of hatched chicks. It is, however, not entirely certain that a manipulation of sex did take place. If food availability is very unpredictable and manipulation of sex is costly, this might be a waste of energy. To detect a possible manipulation of sex, maternal condition and sex of eggs needs to be examined.

The sex ratio of 15 day old chicks did not differ significantly from even, but the sample was very low, and the trend showed an overproduction of females. According to Fisher (1930) it would pay off to produce the rarest sex, thus in this situation a further investment in female broods might not give higher fitness for the parents because many females would, after sexual maturity, not be able to get a partner. However, if the adult survival is lower for females, as documented for many species (see review in Donald 2007), the optimal strategy would be an overproduction of females. This also needs further investigation.

There were no parents that managed to raise three chicks in any of the three breeding seasons at Hornøya, and the total chick survival per brood was less than 1 chick every year. The hatching weight of chicks was positively correlated with the probability of survival, and the hatching weight was significantly lower for chick three. The sex and survival of offspring was not possible to relate to hatching sequence because of small sample sizes. However since the youngest chick in a brood of 3 has a lower weight and survival, a pattern which also have been documented in other studies (Davis & Quinn 1997; Hébert & Barclay 1986), it is very likely that this was the first chick to die on Hornøya too.

In conclusion the three years when this study was carried out the breeding season for herring gulls at Hornøya was bad and many chicks died even during the first days after hatching. Since chicks in all-female broods did have a higher survival than both chicks in all-male and mixed broods, these results support the energy demand hypothesis. However the high mortality of chicks made it difficult to examine in any detail the effect of sibling competition on the survival of male and female offspring. It would be interesting for further studies to investigate whether the brood sex composition have different effect on the chick survival under different environmental conditions.

References

Arroyo B. 2002. Sex-biased nestling mortality in the Montagu`s harrier *Circus pygargus*. Journal of Avian Biology 33: 455-460.

Badyaev A.V., Hill G.E., Beck M.L., Dervan A.A., Duckworth R.A., McGraw K. J., Nolan P.M. and Whittingham L.A. 2002. Science, 295:316-318.

Blanco G., Martínez-Padilla J., Serrano D., Dá Vila J.A. and Viñuela J. 2003. Mass provisioning to different-sex eggs within the laying sequence: consequences for adjustment of reproductive effort in a sexually dimorphic bird. Journal of Animal Ecology. Volume 72: 831-838.

Bogdonova M.I., Nager R.G. and Monaghan P. 2007. Age of the incubating parents affects nestling survival: an experimental study of the herring gull *Larus argentatus*. Journal of Avian Biology, 38:83-93.

Bradbury R.B. and Griffiths R. 1999. Sex-biased nestling mortality is influenced by hatching asynchrony in the Lesser Black-backed Gull *Larus fuscus*. Journal of Avian Biology, 30:316-322.

Bukacinska M., Bucasinski D. and Spaans A.L. 1996. Attendance and diet in relation to breeding success in herring gulls (*Larus argentatus*). The Auk, 113:300-309.

Cameron-MacMillian M.L., Walsh C.J., Wilhelm S.I. and Storey A.E. 2007. Male chicks are more costly to rear than females in a monogamous seabird, the common murre. Behavioral Ecology, 18:81-85.

Clutton-Brock T.H. 1986. Sex ratio variation in birds. IBIS, 128:317-329.

Clutton-Brock T.H., Albon S.D. and Guinness F.E. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature, 313:131-133.

Davis J. and Quinn J.S. 1997. Distribution of parental investment and sibling competition in the herring gull, Larus argentatus. Behaviour, 134:961-974.

Dijkstra C., Daan S. and Buker J.B. 1990. Adaptive seasonal variation in the sex ratio of kestrel broods. Functional ecology, 4:143-147.

Dijkstra C., Daan S. and Pen I. 1998. Fledgling sex ratios in relation to brood size in size-dimorphic altricial birds. Behavioral Ecology, 9: 287-296.

Donald P. F. 2007. Adult sex ratios in wild bird populations. IBIS, 149:671-692.

Drummond H., Osorno J.L., Torres R., Chavelas C.G. and Larios H.M. 1991. Sexual size dimorphism and sibling competition: implications for avian sex ratios. The American Naturalist, 138:623-641.

Erikstad K.E., Fauchald P., Tveraa T. and Steen H. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. Ecology, 79:1781-1788.

Fargallo J.A., Polo V., de Neve L., Martín J., Dávila J.A. and Soler M. 2006. Hatching order and size-dependent mortality in relation to brood sex ratio composition in chinstrap penguins. Behavioral Ecology, 17:772-778.

Fisher R.A. 1930. The genetical theory of natural selection. Claredon Press, Oxford.

Griffiths R. 1992. Sex-biased mortality in the Lesser Black-backed Gull *Larus fuscus* during the nestling stage. IBIS, 134:237-244.

Griffiths R., Double M.C., Orr K. and Dawson R.J.G. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071-1075.

Haftorn S. 1971. Norges fugler. Universitetsforlaget, Oslo/Bergen/Tromsø.

Hébert P.N. and Barclay R.M.R. 1986. Asynchronous and synchronous hatching: effect on early growth and survivorship of Herring Gull, *Larus argentatus*, chicks. Canadian Journal of Zoology, 64:2357-2362.

Hillström L., Kilpi M. and Lindström K. 2000. Is asynchronous hatching adaptive in herring gulls (*Larus argentatus*)? Behavioral Ecology and Sociobiology, 47:304-311.

Kadlec J.A., Drury Jr. W.H. and Onion D.K. 1969. Growth and mortality of herring gull chicks. Bird Banding, 40:222-233.

Kalmbach E., Nager R.G., Griffiths R. and Furness R. W. 2001. Increased reproductive effort results in male-biased offspring sex ratio: an experimental study in a species with reversed sexual size dimorphism. Proceedings of the Royal Society of London series B-Biological Sciences, 268:2175-2179.

Kim S.-Y. and Monaghan P. 2006. Sex of the first hatched chick influences survival of the brood in the herring gull (*Larus argentatus*). Journal of Zoology, 270:116-121.

Komdeur J. 1996. Facultative sex ratio bias in the offspring of Seychelles warblers. Proceedings of the Royal Society of London series B-Biological Sciences, 263:661-666.

Laaksonen T., Fargallo J.A., Korpimäki E., Lyytinen S., Valkama J. and Pöyri V. 2004. Year- and sex-dependent effects of experimental brood sex ratio manipulation on fledging condition of Eurasian kestrels. Journal of Animal Ecology, 73:342-352.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London.

Love O.P., Chin E. H., Wynne-Edwards K. E. and Williams T. D. 2005. Stress hormones: a link between maternal condition and sex-biased reproductive investment. The American Naturalist, 166:751-766.

Malling-Olsen, K.M. and Larsson, H. 2003. Gulls of Europe, Asia and North America. A & C Black Publishers LTD, London.

Monaghan P., Nager R.G. and Houston D.C. 1998. The price of eggs: increased investment in egg production reduces the offspring rearing capacity of parents. Proceedings of the Royal Society of London series B-Biological Sciences, 265:1731-1735.

Müller W., Kalmbach E., Eising C., Groothuis T.G.G. and Dijkstra C. 2005. Experimentally manipulated brood sex ratios: growth and survival in the black-headed gull (*Larus ridibundus*), a sexually dimorphic species. Behavioral Ecology and Sociobiology, 59:313-320.

Nager R.G., Monaghan P., Griffiths R., Houston D.C., and Dawson R. 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. Proceedings of the National Academy of Sciences of the United States of America, 96:570-573.

Nager R.G., Monaghan P., Houston D.C. and Genovart M. 2000. Parental condition, brood sex ratio and differential young survival: an experimental study in gulls (*Larus fuscus*). Behavioral Ecology and Sociobiology, 48:452-457.

O`Connor R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? Animal Behavior, 26:79-96.

Oro D., Jover L. and Ruiz X. 1996. Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin`s gull *Larus audouinii*. Marine Ecology Progress Series, 139:19-29.

Pugesek B.H. 1990. Parental effort in the California gull: tests of parent-offspring conflict theory. Behavioral Ecology and Sociobiology, 27:211-215.

Pugesek B.H. and Diem K.L. 1990. The relationship between reproduction and survival in known-aged California gulls. The Ecological Society of America, 71:811-817.

Royle N.J., Surai P.F., McCartney R.J. and Speake B.K. 1999. Parental investment and egg yolk lipid composition in gulls. Functional Ecology, 13:298-306.

Røskaft E. and Slagsvold T. 1985. Differential mortality of male and female offspring in experimentally manipulated broods of the rook. Journal of Animal Ecology, 54:261-266.

Torres R. and Drummond H. 1997. Female-biased mortality in nestlings of a bird with size dimorphism. Journal of Animal Ecology, 66:859-865.

Torres R. and Drummond H. 1999. Variably male-biased sex ratio in a marine bird with females larger than males. Oecologica, 118:16-22.

Trivers R.L. and Willard D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science, 179:90-92.