Selected aspects of reproductive behavior of the black-headed gull (*Larus ridibundus*)

Radka Piálková




Department of Zoology
Faculty of Science
University of South Bohemia
České Budějovice
Czech Republic

SELECTED ASPECTS OF REPRODUCTIVE BIOLOGY OF THE BLACK-HEADED GULL (*LARUS RIDIBUNDUS*)

RADKA PIÁLKOVÁ

PhD. Thesis

supervisor:
RNDr. Roman Fuchs, CSc.
Department of Zoology, Faculty of Science, University of South Bohemia,
České Budějovice, Czech Republic.

consultant:
Doc. Ing. Marcel Honza, PhD.
Department of Avian Ecology, Institute of Vertebrate Biology,
Academy of Sciences, Brno, Czech Republic

České Budějovice
2009

Piálková R., 2009. Selected aspects of reproductive biology of the black-headed gull (*Larus ridibundus*). Ph.D. thesis, in English, – 82 pp. University of South Bohemia, Faculty of Science, České Budějovice, Czech Republic.

Annotation:
This thesis is focused on two aspects of the reproductive behavior of the black-headed gull (*Larus ridibundus*), a socially monogamous and colonially breeding species. First, the genetic mating system of this species was analyzed using microsatellite markers with focus on the presence of extra-pair paternity and conspecific brood parasitism as a alternative reproductive tactics in both males and females. In case of conspecific brood parasitism a series of experiments with mimetic and non-mimetic eggs was further conducted to explore the ability of the black-headed gull to respond to the occurrence of brood parasitism. Second, we examined the primary sex ratio and its adaptive variation in this species with respect to selected environmental factors, and factors related to the female and chick/egg.

Key words: extra-pair paternity, conspecific brood parasitism, sex ratio, black-headed gull

Financial support:
This study was supported by grants from the Ministry of Education of the Czech Republic: grant (FRVŠ) 1069/2004 and grant (MŠMT) no. 6007665801, by a grant from the Grant Agency of University of South Bohemia (GAJU) no. 51/2003/P-BF, and by a grant from the Grant Agency of the Czech Republic (GAČR) no. 206/05/H012. Financial support of the co-authors and other contributions to individual manuscripts are given in appropriate acknowledgements.

Declaration of author:

I declare that this thesis has been fully worked out by myself and the named co-autors with the use of the cited references.

I further declare, in accordance with the Czech legal code § 47b law No. 111/1998 in its valid version, my consent to the electronic publication of my Ph.D. thesis (after removing marked parts archived by the Faculty of Science) in the publically accessible STAG database that is maintained on web pages of the University of South Bohemia in České Budějovice.

České Budějovice, 27.12. 2009

Radka Piálková

LIST OF PAPERS

This thesis is based on the following papers which are referred to in the text by their roman numerals.

I Character Ležalová R, Tkadlec E, Oborník M, Šimek J, Honza M 2005. Should males come first? The relationship between offspring hatching order and sex in the black-headed gull *Larus ridibundus.* Journal of Avian Biology 36: 478 – 483.

II Ležalová-Piálková R, Honza M 2008. Responses of Black-headed Gulls *Larus ridibundus* to conspecific brood parasitism. Journal of Ornithology 149: 415-42.

III Ležalová-Piálková R. Molecular evidence for extra-pair paternity and intraspecific brood parasitism in Black-headed Gull. *manuscript submitted to Journal of Ornithology*

CONTENTS

Introduction 8

General introduction 8

Sex-ratio 8

Extra-pair paternity 18

Conspecific brood parasitism 23

Present study 27

References 29

Paper I 40

Paper II 54

Paper III 68

Acknowledgements 81

INTRODUCTION

GENERAL INTRODUCTION

I. SEX RATIO

Sex allocation theory predicts that parents should benefit from the ability to control their relative investment in male and female offspring if their profitability sometimes varies (Charnov 1982). This idea has received strong support from studies on those taxa that have precise and well understood mechanisms for the adjustment of offspring sex ratios, especially some haplodiploid insects (Hamilton 1967, Hardy 2002). However, this facultative adjustment of offspring sex was not believed to occur in birds, and it was suggested that this reflected a constraint imposed by the Mendelian process of meiosis.

An increasing number of recent empirical and experimental studies based on molecular sexing techniques (Ellegren and Sheldon 1997, Griffiths et al. 1998) that allow accurate estimations of primary sex ratios, show an apparent control of sex ratios at hatching in birds (review in Clutton-Brock 1986, Hasselquist and Kampeaners 2002, Komdeur and Pen 2002). These studies show a wide range of correlates of sex ratio variation in birds, and reveal how well they can be explained by the standard sex allocation models. However, the exact physiological or genetic mechanisms involved in facultative sex ratio allocation in birds remain largely unknown (Krackow 1995, Sheldon 1998).

1. Potential mechanisms of primary sex ratio manipulation in birds

Recent studies have provided new clues to a potential mechanism that could allow birds to selectively adjust the sex of an egg in response to a number of variables (Pike and Petrie 2003). However, there have been no studies to aimed solely at explaining these mechanism(s), and while there is no evidence as yet, it is possible that a considerable number of potential mechanisms may exist which may not be conserved across all avian orders. Differences in life-history traits between species may have lead to evolution of different sex control mechanisms of sex control (Pike and Petrie 2003). These potential mechanisms involved in facultative sex ratio allocation can be present from the time of follicular formation to egg laying – the time period when maternal control of primary sex ratio can occur (Alonso-Alvarez 2006).

1.1. Preovulation control

Follicular development

Two potential mechanisms may be present during follicular development: a differential rate of follicle development, and follicular atresia (degeneration and resorption during development).

Differential developing rate of follicles

The development of follicles can differ between the follicles leading to male and female gametes (Pike and Petrie 2003). The follicular growth rate could be regulated by hormones (Johnson 2000), which may decrease during the season or within a clutch. This could explain sex ratio variability described in some species (e.g. crimson rosella *Platycercus elegans*, Krebs et al. 2002, black-headed gull *Larus ridibundus*, Ležalová et al. 2005).

Badyaev et al. (2005) demonstrated that pre-ovulation oocytes producing males or females can differ in their growth rates in house finches (*Carpodacus mexicanus*), which is in contrast with the traditional view of the existence of a strict hierarchical oocyte order in the pre-ovulation developement phase (Johnson 2000). These differences in follicle growth rate could lead to changes in the ovulation pattern (Badyaev et al. 2005) and the original oocyte order would not be respected at the time of ovulation, allowing a flexible control of sex ratio. However, there is still the question of how mothers can distinguish between male and female oocytes at pre-meiotic stages and then induce differential growth. Badyaev et al. (2005) found that female androgen and prolactin circulating levels are correlated with offspring sex: higher androgen and lower prolactin concentrations were present when an oocyte became a male. Since variation in follicle growth rate would mean different degrees of exposure to circulating hormones, male and female follicles with different growth rates would also accumulate different concentrations of these hormones in the yolk (Alonso-Alvarez 2006) as was shown e.g. in peafowls (*Pavo cristatus* Petrie et al. 2001) or domestic hens (*Gallus g.s domesticus* Müller et al. 2002).

Selective atresia

Sex-specific atresia could act among follicles in the pre-hierarchical phase (Pike and Petrie 2003), and such a mechanism would save both time and energy. The atresia of hierarchical follicles can be induced hormonally. As with all processes involved in egg production, follicular development and yolk deposition are under the control of maternal hormones (Johnson 2000), and consequently their regulation may be precisely controlled by the laying female.

Segregation distortion

The non-random segregation of sex chromosomes at meiosis has been described in some insects (review in Hardy 2002). In avian sex manipulation, this process refers to the unequal transmission of Z and W chromosomes to germ cells produced by a heterogametic female. Non-random segregation could be the most efficient mechanism of sex ratio manipulation in terms of costs and benefits, avoidind the loss of energy and time associated with other mechanisms (Oddie 1998). In the chicken (*Gallus domesticus*), the sex of the gamete is determined shortly before ovulation, during the first meiotic division (Sturkie 2000). One hypothetical mechanism for gender manipulation is for the chromosome of the preferred sex to be actively assigned to the ovum and the rejected one sent to the polar body (Alonso-Alvarez 2006). On the other hand, Krackow (1999) argues that centrosomes should be randomly assigned to either ovum the or polar body before chromosome segregation, and thus the production of an ovum bearing the desired sex chromosome can not occur. However, the biochemical parameters regulating chromosome segregation in meiosis are still poorly known (Alonso-Alvarez 2006). Recent correlational and experimental findings suggest that yolk and circulating hormones could lead to segregation distortion. It has been shown that the yolk of male eggs can contain higher androgen concentrations than yolk of female eggs (Petrie et al. 2001). The effects of testosterone was found e.g. in peafowls (*Pavo cristatus*, Petrie et al. 2001), spotless starlings (*Sturnus unicolor,* Veiga et al. 2004) or zebra finches (*Taeniopygia guttata,* Rutkowska and Cichón 2006). The effect of corticosterone was demonstrated in japanese quail (*Coturnix c. japonica*, Pike and Pertie 2006) and progesterone in the domestic chicken (*Gallus gallus,* Correa et al. 2005).

Selective resorption and ovulation

Selective resorption would allow females to abort and subsequently reabsorb post-meiotic ova containing unwanted sex chromosomes prior to ovulation (Elmen 1997) (this is in contrast to atresia, which refers to the reabsorption of pre-meiotic follicles). This mechanism would cause an approximate 24 hour gap in the laying sequence. Consequently, selective resorption is most likely to occur in species which lay clutches of one or two eggs. Such species can avoid the costs suffered by species which lay larger clutches, where the gap caused by waiting for the right sex would greatly prolong the duration of laying (Emlen 1997). This mechanism could potentially be at work for the two species – seychelles warbler (*Acrocephalus sechellensis*, Komdeur et al. 1997) and eclectus parrot (*Eclectus roratus,* Heinsohn et al. 1997) - for which there is evidence that manipulation takes place prior to laying, and interestingly, both lay no more than two eggs in a clutch.

Selective ovulation refers to a situation when the ovum fails to be picked up by the infundibulum and ends up in the abdominal cavity where it is subsequently reabsorbed. This can be detected when the number of eggs laid does not correspond to the number of postovulatory follicles in the ovary, as observed e.g.

in domestic chickens (Sturkie 2000). However, this internal ovulation could also cause peritonitis, which can be fatal and therefore is expected to be avoided (Sturkie 2000).

1.2. Postovulation control

Sex-specific fertilization

An ovum spends about 15-30 min in the infundibulum, during which it is fertilized (Sturkie 2000) using sperm released from sperm-storage tubules located in the utero-vaginal region of the female (Birkhead and Møller 1992). Following the oviposition of each egg, sperm are released from the tubules by an unknown mechanism to fertilize them. The selective fertilization of ova bearing particular sex chromosome would provide a mechanism by which the female could control the sex of a laid egg (Pike and Petrie 2003). Nevertheless, this seems impossible, because sperm are released from the tubules before the time of ovulation and sex determination (Birkhead and Møller 1992). However, in some species the amount of sperm in tubules decreases dramatically after a single fertilization event, and repeated copulation may be required to ensure fertilization of the next ovum (Alonso-Alvarez 2006). In such cases, females could avoid copulation when the oocyte is of the unwanted sex. Pike and Petrie (2003) suggested several other mechanisms of sex specific fertilization: First, a female could affect the motility of the released sperm by changing the environment of the oviduct (pH, viscosity of fluids, temperature). Second, a female could change the composition of the ovum membrane, preventing the penetration of spermatozoa. Third, a female could inhibit zygote development after the sperm penetrate the oocyte. Fourth, there is the possibility that the process is indirectly under the control of the father – it may be that the sperm themselves are selective as to which sex of ova they inseminate.

In any case, all these potential mechanisms are expensive ways to control for sex, leading to laying gaps or unfertile eggs since the reabsorbtion of yolk is less likely at this late stage (Sturkie 2000).

Sex-specific post-laying embryo mortality

There is another possible potential mechanism acting in sex control - sex bias in embryo mortality. The cost of this sex ratio manipulation should be large because materials and energy invested in deceased eggs will be lost. However, the relative costs will depend on the clutch size. Species with larger clutches will not suffer as high costs as those species with a single egg per clutch. Cichón et al. (2005) described higher mortality rates for male embryos from unhatched eggs in three passerine species. Sex- embryo mortality could act through female-specific provisioning of the egg with substances enhancing or reducing development of the embryo, either with the desired sex or irrespective of egg sex.

Sex-specific manipulation of egg composition

A sex-specific maternal manipulation of egg composition could lead to differential survival rates for male and female embryos. There are a number of substances commonly found in egg yolk that may be important in sex-biased favouritism. In addition to the presence of egg components such as lipids and proteins (Royle et al. 1999, Nager et al. 2000), carotenoids (Blount et al. 2002) and antibodies (Gasparin et al. 2001), there are also certain quantities of maternally derived hormones (Schwabl 1993, Petrie et al. 2001, Bonnier et al. 2007). A specific allocation of resources to a specific egg would depend on the female´s ability to recognize the sex of each gamete from the moment of sex determination (meiosis I) and, as yet there is no such evidence of maternal embryo sex recognition in birds (Alonso-Alvarez 2006).

Non-sex-specific manipulation of egg composition

Females could manipulate egg composition by investing equally in all eggs, independent of sex, because any substance added to the eggs could interact differently with male and female embryos (depending on the sex-differential production of unique gene products in embryonic development) and result in differential mortality. Recent experiments suggest that increased levels of maternal hormones differentially affect embryo survival. For example, female zebra finches injected with testosterone produced male eggs with lower hatching success than female eggs (Rutkowska and Cichón 2006). Egg composition could also interact with other embriomic sex-specific traits. Some studies suggest that the duration of embryo development can differ between sexes. In eurasian kestrels (*Falco tinnunculus)*, female embryos had shorter embryonic periods and hatched sooner than males (Blanco et al. 2003), while the opposite is true in guillemots (*Ceppus grylle*, Cook and Monaghan 2004).

Sex-specific incubation and dump-laying

Pike and Petrie (2003) also suggested that egg-size dimorphism could be used as a cue in sex-selective incubation, which could lead to sex-specific mortality. However, as in the case of sex-related survival of chicks, such a mechanism would work exclusively on the secondary sex ratio.

2. Adaptive models of sex allocation

There are four main classes of models providing adaptive explanations of sex ratio patterns in birds.

2.1. Frequency-dependent sex allocation

Fisher´s hypothesis

Fisher’s theory of equal investment (Fisher 1930) predicted that population sex ratio biases are returned to equality because of a frequency-dependent reproductive advantage for the rarer sex. Fisher's argument is that in a population with a biased sex ratio, offspring belonging to the rarer sex have better mating prospects than those belonging to the more common sex. Later modifications of Fisher's model deal with the ratio of investment required to produce the sexes rather than to the numerical sex ratio. Hence, if one sex were twice as costly to produce as the other, it would be produced half as frequently: the numerical ratio would be biased but the investment ratio would not.

2.2. Condition-dependent sex allocation

Trivers-Willard hypothesis

Trivers and Willard (1973) proposed that when one sex gains more than the other from extra parental investment, parents with relatively more resources to invest (e.g. parents in good condition) will bias their allocation toward the sex with the greater rate of reproductive returns. This theory was developed for polygynous species, where one male can monopolize the reproduction of many females and many other males will fail to reproduce. Hence the variance in reproductive success among males will be much greater then the variance among females. If a female is able, via her investment, to influence the success of her offspring, then females in good condition are more likely to produce males, while females in poor condition are more likely to produce daughters.

Theory of sexy sons - Attractiveness hypothesis

The first evidence of the attractiveness hypothesis came from a study on zebra finches (*Poephila guttata*), where females pair preferentially with attractive males (Cockburn et al. 2002). Females paired to attractive males are more likely to invest in sons, whereas females paired with less attractive males invest in daughters. This hypothesis extends the classic Trivers-Willard logic in two ways. First, the prerequisite of polygyny in the Trivers-Willard hypothesis is removed, and second, it suggests that the attractiveness of a partner could motivate females to invest differently in their offspring.

2.3. Condition-dependent sex allocation

Local mate competition hypothesis (LMC)

This theory was put forward by Hamilton (1967), and was the first to consider the effects of group structure on the sex ratio. It considers environments where a number of individuals colonize a habitat and their offspring mate amongst themselves, before the daughters disperse. Unmated daughters and all sons are assumed to not disperse from the natal group. In such situation, the sex ratio should be skewed towards daughters because competition among related males to mate with their sisters increases.

Local resource competition hypothesis (LRC)

The local resource competition hypothesis was originally defined by Clarc (1978) for primates, but it is also valid for birds (Gowaty 1993). In species where one sex remains philopatric, competition for resources between related members of that sex leads to selection for the overproducing of members of the dispersive sex, which do not compete among themselves or with their mother. There are at least three different ways in which LRC can arise in birds: first, through *differential natal philopatry*, so that the philopatric sex which competes directly with parent(s) for resources, becomes more costly. Second, through *differences in the timing of dispersal* such that one sex stays longer in the natal territory before dispersion, and third, through differences in distances of dispersal from natal territories such that likelihood of competition with parents for resources is greater for one sex of offspring than the other (Gowaty 1993).

Local resource enhancement hypothesis (LRE)

Local resource enhancement (LRE) is the converse of LRC. In species where the presence of philopatric offspring enhances the fitness of parents, there may be selection for overproduction of the philopatric sex. This effect has been reported in cooperatively breeding species where the more numerous sex is the helper class (Gowaty and Lennartz 1985, Bednarz and Hyden 1991).

2.4. Sex allocation and the cost of reproduction

Cost of reproduction hypothesis

Where resources for parental investment are limited, parents may manipulate the sex ratio to lower the risk of reproductive failure and/or increase the prospects that they will survive to reproduce again. Therefore, females in poor condition are supposed to produce the „cheaper“sex that imposes lower demands on resources, to minimize the risk of failure or brood reduction, or to reduce costs in terms of future reproductive success. This hypothesis differs from the Trivers-Willard logic and LRC because the impact is on the maternal reproductive value and fitness rather than that of her offspring (Cockburn et al. 2002).

Male exploitation hypothesis

Females exploit differential provisioning of the sexes by males to reduce the costs of parental care. In polygynous species, primary females produce broods biased towards sons while secondary females produce broods biased towards daughters (Westerdahl et al. 2000). In these species, males usually only assist the primary females with nest provisioning; however, this could be because males provide more food to male-biased broods. This male exploitation hypothesis is potentially applicable in any circumstance where males provide different resources to male and female offspring.

3. Potential factors promoting sex manipulation

When there are differences in the fitness returns of producing sons versus daughters, sex allocation theory predicts that selection should favor investment in those offspring with higher reproductive value (Charnov 1982, Frank 1990). Females can manipulate their investment in male and female offspring in respect to numerous factors that, potentially, can have sex-specific effects on offspring fitness (review in Clutton-Brock 1986, Frank 1980, Sheldon 1998, Hasselquist and Kampeaners 2002, Komdeur and Pen 2002, Pike and Petrie 2003, Alonzo-Alvarez 2006). Such factors include those related to four major categories: the quality of the parents, the quality of the external environment, the quality of the social environment, and number and asymmetry among the offspring (Tab.1).

3.1. Parental quality

The environment that parents provide for their offspring can affect their reproductive value differentially and therefore cause selection for variable sex allocation (Trivers and Willard 1973). This suggestion can be applied to any quality which parents transmit to offspring, not only those of female origin (Sheldon 1998). For example, if male attractiveness is related to male reproductive success, and if these traits are inherited by sons, then sons of attractive males might be of higher reproductive value than the daughters of such males. The reverse would be true for the offspring of less attractive males. It has been argued that it would therefore be adaptive to modify sex ratios in response to male attractiveness (Ellegren et al. 1996, Svensson and Nilsson 1996, Sheldon et al. 1999, Griffith et al. 2003, Pike and Petrie 2005).

3.2. External environment

Several studies have reported seasonal variation in offspring sex ratios. This variation is supposed to be attributed to increasing differential mortality biased towards the larger sex due to decreasing food availability during the season (Komdeur and Pen 2002). Such seasonal sex ratio trends seem to be common among raptors (Dijkstra et al. 1990, Korpimäki et al. 2000, Zijlstra et al. 1992, Daan et al. 1996) and owls (Appleby *et al.* 1997). The seasonal variation in sex ratio can be also linked to sex-differential timing of the first breeding attempt. It has been shown that the probability of starting breeding as a yearling may decrease with birth date for males, but not for females (Komdeur et al. 2002).

3.3. Social environment

In cooperatively breeding species, where the tendencies of offspring to be helpful are sex-specific, selection is expected to favor biased sex ratios towards the more helpful sex (Gowaty and Lennertz 1985, Komdeur 1994, Komdeur et al. 1997, Ligon and Ligon 1990, Legge et al. 2001). But, having helpers can be costly for parents inhabiting poor territories, because helpers deplete food resources, but is beneficial to parents (through higher reproductive success) inhabiting rich territories (Komdeur 1994). However, other studies have not found any significant facultative sex ratio adjustment toward the helpful sex (Koenig et al. 2001, Rathburn and Montgomerie 2004).

3.4. Sexual size dimorphism

In sexually size dimorphic species, size differences between sons and daughters are likely to reflect sex-specific costs to the parents (Anderson et al. 1993, Krijgsveld et al. 1998). The larger sex is assumed to be more costly because of its presumed higher food requirements (Wiebe and Bortolotti 1992), and is usually more vulnerable and suffers higher mortality than the smaller sex. Also, one sex may by more costly to produce than the other, for example, because it has a higher metabolic rate, grows faster, or begs more (Hasselquist and Kampeaners 2002).

When the costs of rearing males and females differ, the offspring sex ratio is expected to be biased toward the less expensive sex. Such facultative manipulation of offspring sex gives parents the potential to fine-tune the number and quality of offspring to prevailing circumstances, thereby maximizing parental fitness (Nager et al. 1999).

Table.1. Overview of the potential factors promoting sex ratio manipulation

factors with the potential effect on sex ratio	references
parents	
parental condition	Wiebe and Bortolotti 1992
parental age	Sheldon et al. 1999
parental breeding experience	Weimerskirch et al. 2000
male	
male plumage colour	Sheldon et al. 1997, Sheldon et al. 1999
male attractiveness	Ellegren et al. 1996, Griffith et al. 2003, Pike 2005, Pike and Petrie 2005
male survival	Svensson and Nilsson 1996
male body size	Kölliker et al. 1999
female	
female condition	Bradbury and Blakey 1998, Nager et al. 1999, Kalmbach et al 2001, Clout et al. 2002, Velando 2002, Alonzo-Alvarez and Velando 2003, Whittingham et al. 2005

female age	Blank and Nolan 1983, Sheldon et al. 1997
female breeding experience	Gowaty and Lennartz 1985
female size	Wiebe and Bortolotti 1992
female harem status	Nishiumi et al. 1996, Westerdahl et al. 1997, Nishiumi 1998, Westerdahl et al. 2000
female circulating level of testosterone	Veiga et al. 2004, Rutkowska and Cichon 2006
female circulating level of corcicosterone	Pike and Petrie 2006
female circulating level of progesterone	Correa et al. 2005
environmental and social	
laying date	Howe 1977, Dijkstra et al. 1990, Zijlstra et al. 1992, Daan et al. 1996, Lessells et al. 1996, Tella et al. 1996, Smallwood and Smallwood 1998, Torres and Drummond 1999, Krebs et al. 2002, Velando et al. 2002
stress	Myers 1978
food availability or quality	Wiebe and Bortolotti 1992, Appleby et al. 1997, Bradbury and Blakey 1998, Kilner 1998, Rustein et al. 2004
habitat quality	Decoux 1997, Julliard 2000
territory quality	Komdeur et al. 1997, Komdeur 1998
territory availability	Komdeur 1998
number of helpers	Ligon and Ligon 1990, Komdeur et al. 1997, Legge et al. 2001
offspring	
laying order	Fiala 1981, Ryder 1983, Ležalová et al. 2005, Müller et al. 2005, Krebs et al. 2002
clutch size	Gowaty 1991, Gowaty 1993, Lessells et al. 1996, Heinsohn et al. 1997, Dijkstra et al. 1998
sex-differential dispersal	Fiala 1981
sexual size dimorphism	Howe 1977, Bednarz and Hayden 1991, Nishiumi et al. 1996, Westerdahl et al. 1997, Nishiumi 1998, Oddie 2000,
hatching synchrony	Lessells et al. 1996, Bradbury and Griffiths 1999

II. EXTRA-PAIR PATERNITY

Genetic monogamy refers to an exclusive mating relationship between a male and a female. In contrast, social monogamy refers to an association between a male and female for the purpose of reproduction, and the mating relationship is not necessarily exclusive. Griffith et al. (2002) indicate that less than 25% of socially monogamous bird species studied practice true genetic monogamy.

Copulations outside the pair bond during the fertile period, referred to as extra pair copulations (EPCs), are widespread among avian taxa in both socially monogamous and polygynous birds. The relative frequency of multiple copulations by a female may be affected by social organization and the mating system simply because variation in the temporal and spatial distribution of females may be an important determinant of copulation frequency with multiple males. Socially breeding species are predicted to engage in EPCs with higher frequency than solitary breeding species (Møller and Birkhead 1993). The close proximity of many neighbors may enhance the probability of EPCs leading to extra pair fertilizations (EPFs).

In addition, the method a male bird uses to insure paternity may significantly affect the frequency of extra- pair paternity (EPP). Two main methods exist – mate guarding and frequent within-pair copulations (Birkhead et al. 1987). Frequent copulation is generally used as a paternity guard in those birds in which mate guarding, where the male closely monitors the female is not practical. Such is the case with many colonial species, where one member of the pair usually remains at the nest and defends the territory while the other forages away from the colony. Frequent copulation may be potentially an effective paternity guard for two reasons: first, the probability of fertilization increases with the number of sperm delivered by a male; and second, frequent copulation is efficient, since it is generally fertilization advantage to the last male to copulate with female just before fertilization (Birkhead and Møller 1998). It has been supposed, however, that in most bird species females likely control the success of each copulation attempt and sperm transfer (Petrie and Kempenaers 1998). Even so, despite these paternity guards the frequency of EPP can by very high in some species.

A variety of the potential direct and indirect costs and benefits of EPF could affect both sexes. Below, I briefly discuss what are currently thought to be some of the major benefits and costs of participating in EPC, which may lead to EPP.

1. Benefits of extra-pair paternity

1.1. Benefits to males

The direct benefit to males is an increase in reproductive success; maximizing the number of copulation partners is an obvious strategy to promote fitness. Those males fertilizing the most eggs will sire the most offspring. By producing essentially cost free genetic offspring, males can greatly increase their reproductive success, both per year and over their lifespan.

1.2. Benefits to females

The benefits arising from seeking EPC differ between the sexes. Females do not realize the benefits of an increased number of offspring, but rather may seek EPC to obtain direct (non-genetic) or indirect (genetic) benefits for their offspring. The potential benefits to a female can be divided into three general categories: material, genetic, and social.

Material benefits

Females may gain some direct benefits from seeking EPC through increased access to material resources, e.g. foraging opportunities, parental care, or extra protection against nest predators (Gray 1997).

Social benefits

Sexual encounters in both reproductive and non-reproductive contexts can provide some benefits to females. These hypothesized benefits do not necessarily require fertilization, so EPCs can also take place outside the fertile period. In terms of social profit, the act of seeking and participating in EPC may allow females a chance to assess males, either as prospective future mates or as EPC partners during the next breeding season. Females may also seek EPC to reduce the costs of mate loss enabling them more quickly replace a lost partner with an extra-pair partner. This scenario is supposed to play a role in species or populations where mortality between breeding attempts or divorce rate are high (Cézilly and Nager 1995).

Genetic benefits

Fertility

Females may seek EPP in order to guard against infertility in their own social mate. In species where females lay only one egg per year, this fertility insurance may be very important (Wagner 1992).

Good genes

The good genes (genetic quality) hypothesis can account for females of monogamous or polygynous species that are mated to “poor quality” males. Females may seek EPP in order to obtain good genes for their offspring from a morphologically or physiologically superior male, thereby increasing the attractiveness and/or viability of at least some of their offspring. Also, a male’s relative dominance can affect females in their choice of an EPP partner. According to this theory, females mated to top-quality males should tend to avoid EPC, while females mated to males below the average should seek them.

Genetic diversity

The hypothesis of genetic diversity suggests that females seek EPP to maximize genetic diversity among their offspring (Westneat et al. 1990). However, females are not able to estimate the genetic similarity between themselves and prospective males, therefore the distribution of EPP among females is random. For example, in an unpredictable environment genetic diversity might increase the chance that at least some chicks will be successful.

The overall genetic diversity of a population depends on the balance between migration, mutation, selection, size of population, as well as on current ecological factors (Petrie and Kempenaers 1998). Lower genetic variation is expected in isolated populations or in populations that have currently gone through a bottleneck and in such populations a low frequency of EPP is also expected.

Genetic compatibility

One version of this hypothesis proposes that females would gain from increased heterozygosity in their offspring because the probability that lethal or deleterious recessive alleles are expressed is reduced (Brown 1997). Genetic incompatibility between partners can also arise as a consequence of various agents of intragenomic conflict and other forces acting at the suborganismal level leading to less- or non-viable zygotes (Kempenaers et al. 1999).

2. Costs of extra-pair paternity

2.1. Costs to males

Participation in extra-pair activity might entail a trade-off between seeking EPCs and investing in mate guarding and parental care. Apart from these potential trade-offs, the costs to males also include sperm depletion, increased risk of cuckoldry, risk of parasite or disease transmission, and divorce. Of these, only one – the risk of cuckoldry, is considered to be important as males cannot effectively guard their own mates and seek EPCs (Petrie and Kempenaers 1998).

2.2. Costs to females

The main cost of EPP to a female is considered to be the loss of male’s help in rearing offspring. However, if males respond to cuckoldry by reducing investment in offspring, the cost to female may vary. Gowaty (1996) has suggested that female mating strategy is based on the degree to which they rely on male parental care for the rearing of their offspring – the “Constrained female theory”. Females in poor condition and in low quality environments are thus supposed to be faithful to their social partner, because they have the most to lose. However, there are other possible costs of EPP to females, such as potentially increased exposure to sexually transmitted disease or costs associated with searching and assessing extra-pair males. The costs of finding an additional male can be costly both in terms of the time and energy spent on searching. Female also have to be able to assess the quality of available males in order to avoid fertilization by a low or unknown quality male (Petrie and Kempenaers 1998).

3. Patterns of extra-pair paternity

Despite the large number of studies devoted to understanding the evolution of extra-pair paternity in birds there is still great inconsistency in the results, and many hypotheses have been proposed to explain the observed variations in EPP levels (Westneat and Sherman 1997, Møller and Ninni 1998, Griffith et al. 2002, Neudorf 2004).

Phylogenetic correlation - Bennett and Owens (2002) have revealed that ancient phylogenetic diversifications in birds explain a substantial proportion of the variation in interspecific levels of EPP. Arnold and Owens (2002) showed that more than the 50% of the interspecific variance is located at the taxonomic family level or above, which indicates that temporary ecological factors must have a secondary role. The evolution of fast life histories (e.g., low adult survival, high fecundity, and little parental care) is also linked to these divisions in phylogeny. Bennett and Owens (2002) suggest that species predisposed to fast life histories necessarily have high levels of EPP.

However, to date most attempts to explain interspecific variation in the rates of extra-pair paternity have been largely dominated by two ecological factors – breeding synchrony and breeding density. There has been an ongoing debate about the effect of breeding synchrony on extra-pair mating strategies (Neudorf 2004). There are two hypotheses: first, “synchrony hypothesis” (Stutchbury and Morton 1995) claims that breeding synchrony promotes EPP. The argument is that synchronous breeding allows females to more effectively compare potential extra-pair males. Males, on the other hand, should benefit from the availability of fertilizable females, which would increase the opportunity for EPC. The second hypothesis - “asynchrony hypothesis”, however, claims just the opposite that breeding asynchrony promotes EPP (e.g. Birkhead and Møller 1992). In situations when males guard their mates, asynchronous breeding gives them an opportunity to seek EPC when their own mates are no longer fertile. Although neither of these hypotheses has unequivocal support from empirical studies at the population level, comparative analyses have failed to find a relationship between breeding synchrony and rates of EPP (Bennett and Owens 2002).

Variation in breeding density is one of the most traditional explanations for variation in the EPP rate. Density should promote EPP because of the proximity of potential copulation partners. Colonial species or those species nesting at high densities are predicted to have higher EPP frequencies than species nesting at lower densities. The relationship between breeding density and EPP has been examined in four ways: interspecific analyses across taxa, intraspecific comparison within a population, intraspecific comparison among different individuals within a single population, and meta-analyses of species-species studies (Grifith et al. 2002). No robust evidence has yet been found for the role of breeding density in determining interspecific variation (Westneat and Sherman 1997, Bennett and Owens 2002), and the lack of a consistent relationship has been observed in studies focused on intraspecific comparison between populations (e.g. Yezerinac et al. 1999, Bjørnstad and Lifjeld 1997, Hasselquist et al. 1995). However, the alternative intraspecific approach of making comparisons among individuals in the same population has found positive relationships between breeding density and extra-pair paternity (e.g. Hoi and Hoi-Leitner 1997). Also, as part of comparative study of the link between breeding density and rate of EPP Westneat and Sherman (1997) tested for an overall relationship between populations of the same species. They reported that there was a general trend for high-density populations to have a higher rate of EPP than conspecific populations at lower densities. One approach for testing the role of breeding density in determining the rate of extra-pair paternity is to perform meta-analyses across single-species studies. Such an analysis tests whether there is evidence of a consistent relationship between two or more variables across a series of within species studies (Grifith et al. 2002). Møller and Ninni (1998) investigated a large range of factors that have been suggested to be associated with intraspecific variation in EPP rates. Their results strongly suggest that breeding density is an important factor in determining the variation in EPP rate among individuals in the same study population. To conclude, there is little evidence that interspecific variations in EPP rate are a consequence of variability in breeding density. However, there is good evidence that breeding density may be important in determining the variation in the rate of EPP at lower taxonomic levels.

In addition to the traditional ecological explanations for variation in EPP, ther is also the hypothesis that the EPP rate should be associated with the level of need for parental care. There are two hypotheses regarding how levels of male involvement in parental care may contribute to variation in EPFs among species. First, “trade-off hypothesis” suggests that males may be limited in their pursuit of extra-pair matings because of constraints imposed by caring for offspring (Neudorf 2004). Second, “female-constraint hypothesis” (Gowaty 1996), suggests that males actually reduce care with low paternity certainty. This means that females should be more likely to seek extra-pair copulation when they can rear offspring with little or no help from their partners, and can therefore risk the cost of reduced parental care. Birkhead and Møller (1996) used a species–based comparative approach which showed that, as predicted, rates of EPP tended to be lower in species where male care was essential.

In addition, longevity (annual adult mortality) is a factor predicted to be positively correlated to the rate of EPP among species (Mauck et al 1999). According to this hypothesis males should be more tolerant to low paternity certainty if they have a high probability of mortality and thus low future opportunities for reproduction. Alternatively, if males have future opportunities to breed, they should be more likely to desert females when their paternity is uncertain. In support of this hypothesis, Arnold and Owens (2002) found a significant positive relationship between EPPs and adult annual mortality among species.

III. CONSPECIFIC BROOD PARASITISM

Conspecific brood parasitism is an alternative reproductive tactic in which a female lays eggs in the nest of a conspecific female who provides incubation and takes care of the young. CBP is widespread among birds and the number of species known to employ this tactic is still increasing (Yom-Tov 1980, Yom-Tov 2001). The habit is disproportionately prevalent among precocial species – especially waterfowl, but the long list of species employing CBP also includes semi precocial and altricial species (Yom-Tov 1980, Yom-Tov 2001, Rohwer and Freeman 1989). There are asymmetries in the costs of parasitism to the hosts within this altricial-precocial spectrum. The costs of being parasitized by a conspecific should be high for birds that feed their young, as fostering conspecific eggs can result in a variety of direct and indirect costs for the host parents. In contrast, because parental care can be shared in precocial species, brood parasitism may have lower effects on host reproductive success (Rohwer and Freeman 1989), although it is also not of cost to the host (Dugger and Blums 2001). Generally, CBP may pose costs both before and after clutches hatch. However, several authors have even suggested that parasitism might confer benefits to hosts, especially in species with precocial young (Payne 1977, Eadie et al. 1988, Dickinson 2007). A possible benefit of parasitism to host is higher inclusive fitness, if parasite is relatives (Andersson 1984, Andersson and Åhlund 2000, López-Sepulcre and Kokko 2002). However, if brood parasitism has negative consequences for the host's fitness, parasites should avoid laying eggs in nests of relatives (Zink 2000, Semel and Sherman 2001).

1. Costs of conspecific brood parasitism

1.1. Prehatch costs

Costs before hatching include the need to increase the length of incubation period, reduced hatching success in parasitized nests, and higher rates of nest abandonment. In addition, hosts may even lay fewer eggs when parasitized.

Longer incubation periods may pose energetic costs to hosts in term of increasing the basal metabolic rate more than 2.5 times (Thomson et al. 1998) and may also prolong the exposure of nests to predators and thereby reduce the survival of both hosts and parasite eggs (Nielsen et al. 2006). The predation risk might also increase if parasites increase the amount of activity at the nest. It has also been suggested that longer incubation periods might reduce residual yolk reserves at hatching, causing reduced offspring survival (Hepp et al. 1990).

Lower hatching success could result from incomplete warming of the entire clutch, which also could affect host eggs. The displacement of eggs from parasitized nests which significantly reduces the number of host eggs hatching (Sorenson 1997) is also an apparent effect of parasitism.

Lower host clutch size - parasitic eggs may suppress ovulation by the host (Rohwer and Freeman 1989). The host may reduce own clutch by the number of eggs added by the parasite in order to preserve the hatching success of the host eggs, since incubation of the larger clutch might not be sufficient (Andersson and Ericsson 1982).

The most important cost of nest parasitism (at least for precocial species) seems to be abandonment of the nest. However, for a wide range of parasitism levesl, the costs of remaining with a parasitized clutch are low compared to the costs of abandoning the clutch and laying a replacement clutch (Nielsen et al. 2006).

1.2. Posthatch costs

After hatching, parasitism may affect offspring survival, as well as the survival and future reproduction of the laying female.

Lower nestling recruitment (Andersson and Ericsson 1982) may be caused by increased brood size that negatively affects the success of chicks, so that nestlings either starve or fledge in poor condition and face higher pos-tfledging mortality.

Parents rearing enlarged broods may be less likely to raise another brood during that season, which results in lower reproductive success, or may suffer lower survival rates (Drugger and Blums 2001).

These costs to hosts, both pre- and post-hatching, should cause strong selection for effective defenses against CBP, because even small negative parasitism effects can select for anti-parasite behavior (Sorenson 1997) and start up coevolutionary arms race between parasites and their hosts (Rothstein and Robinson 1998).

However, host defenses are less prominent in conspecific brood parasitism in comparison to interspecific brood parasitism, because CBP is usually less costly and because the host and parasite are usually identical in appearance and behavior, and it may be especially difficult for hosts to develop defenses (and for researchers to identify any that do evolve). Nevertheless, several antiparasite behaviours occur among potential host.

1.3. Host defenses

Among the various possible host defenses to brood parasitism, the recognition and rejection of a parasitic egg is the most appropriate tactic. This is the best-documented defense by hosts to interspecific parasitism (Rothstein and Robinson 1998). However, recognition and rejection of conspecific eggs is supposed to be difficult because of the similarity between the parasitic and host eggs (Rothstein and Robinson 1998). Species facing CBP have developed two features to deal with this egg recognition problem. First, hosts may remove all eggs from the nest, regardless of their appearance, before they start to lay. This strategy does not work in case when CBP occurs after the host has already begun to lay, therefore some species may have evolved extreme variation in egg appearance among their clutches to deal with such parasitism (Jackson 1998). Such high variation helps enable individuals to distinguish between their own eggs and those of conspecifics. As egg recognition is based on color and spotting patterns, this strategy could hardly evolve in species with unicolor eggs (e.g. ducks). In fact, many species as waterfowl show no evidence of recognition or discrimination against parasitic eggs (Sorenson 1997, Drugger and Blums 2001), because discriminating among unicolored eggs with no spotting would probably entail high costs from recognition errors (Davis 2000). Therefore, other behavioral aspects like aggressive nest defense, timing of laying or nest site selection might be under selective pressure due to parasitism (Sorenson 1997).

Indeed, nest guarding and aggressive behavior have been documented as possible strategies for preventing nest parasitism by conspecifics (Petrie and Møller 1991, Rothstein and Robinson 1998). Nest defense and CBP were found to be positively density-dependent (Møller 1998) – guarding intensity increases with size of the colony and thus with the risk of parasitism.

Asynchronous nesting may also decrease the probability of CBP. A female which lay outside the time other females are laying their eggs may decrease the risk of parasitism (Petrie and Møller 1991).

2. The adaptive significance of conspecific brood parasitism

Parental care often confers costs (Trivers 1972, Clutton-Brock 1991), which can be avoided by being parasitic (Payne 1977, Andersson 1984). CBP can be viewed as an alternative reproductive behavior that allows an individual to circumvent the time and energy costs of reproduction. Three individual reproductive tactics to achieve this are expected (Davis 2000). These three strategies are not mutually exclusive, and they may occurr simultaneously in a population depending on current ecological and/or individual physiological conditions and the pay-offs they are likely to receive (Sorenson 1998).

2.1. “The best of a bad job” strategy

In some cases, females are thought to lay their egg in the nests of others if they fail to nest normally. This disruption of the standard nesting cycle may be a consequence of nest destruction by predators, energetic limitations on breeding, nest site competition, bad weather conditions or other forms of disturbance (Sorenson 1998, Davies 2000). In these cases, females might not be able to cope with the energetic demands necessary for a regular re-nesting and might try to salvage at least some success through parasitic laying (Davies 2000).

2.2. Restraint strategy

Females could choose parasitism as an equally profitable alternative to nesting, with parasitic laying representing an adaptive reduction of the reproductive effort (restraint) in response to poor prospects for successful nesting (Sorenson 1991, Sorenson 1998). By laying parasitic eggs instead of nesting themselves, females can avoid all the costs and risks of parental care, and may achieve higher annual fecundity and/or higher annual survival (Yom-Tov 1980, Sorenson 1998).

2.3. Mixed strategy

Females may enhance their reproductive success by adopting a mixed strategy: a combination of regular breeding and parasitism. Females could increase their reproductive success by spreading the risk among several nests, by reducing the competition within their own nests, and by increasing their own fecundity without the need for any extra parental effort (Sorenson 1998, Davis 2000).

3. Patterns of conspecific brood parasitism

Most of hypotheses explaining variation in CBP rates are focused on the association of CBP with the availability of access to the conspecific nest. The highest rates of CBP rates are expected when nests are crowded in small space, i.e. in colonial species or under high nesting densities, and when nesting sites are in short supply (Yom-Tov 1980, Yom-Tov 2001, Rohwer and Freeman 1989). Similarly, Sorenson (1992) and Geffen and Yom-Tov (2001) have suggested that species with limited parental care and large brood sizes may be predisposed to brood parasitism. These hypotheses agree with comparative analyses of variation in the CBP rate by Arnold and Owens (2002) and Bennett and Owens (2002) which showed significant associations with large clutch size, high annual fecundity and short period of chick feeding, but no association with breeding density (Arnold and Owens 2002, Bennett and Owens 2002).

In addition, the proportion of birds showing CBP has been hypothesized to be strongly biased towards those with self feeding (precocial) young versus those with parentally fed (altricial) young (Rohwer and Freeman 1989).

This pattern might occurr primarily because birds with parentally fed young are under intense selective preassure to defend against CBP, while selection for defense is weaker in birds with self feeding young (Rohwer and Freeman 1989). Furthermore, within these two groups, the intensity of CBP seems to depend on contemporary ecological factors such as breeding density or nesting site supply (Arnold and Owens 2002).

PRESENT STUDY

Like other gulls (Laridae), the black-headed gull (*Larus ridibundus*) is a long lived, colonially breeding species with high adult survivorship (Cramp 1983). The standard clutch size of this species is three eggs. Both females and males participate in parental care throughout incubation and chick-rearing, which leads to social monogamy in this species (Cramp 1983). Given these traits, a low frequency of extra-pair paternity (EPP) and conspecific brood parasitism (CBP) might be expected (Arnold and Owens 2002, Bennett and Owens 2002). However, both extra-pair copulations and abnormally large clutches with eggs differing in size, shape or colour, indicating conspecific brood parasitism, have been observed. These observations suggest the presence of alternative reproductive behavior in this species (Paper II, III).

Alternative reproductive behaviors allow individuals to circumvent ecological or social constraints on reproduction (Trivers 1972, Andersson 1984). Although both sexes may adopt alternative behaviors, the nature of the tactics they employ differs due to sexual differences in reproductive constraints. Male reproductive success is typically limited by access to mates, and consequently male alternative reproductive tactics are concerned with increased mating opportunities. To increase their reproductive output, males may seek extra-pair copulations (EPCs) resulting in extra-pair offspring. Paper III deals with EPP in the black-headed gull.

In contrast, female reproductive success is often limited by resources available for reproduction (Trivers 1972), and hence females adopt alternative tactics to bypass reproductive constraints imposed by resource limitation. Conspecific brood parasitism may be a female tactic. Parasitic females parasitize the parental care of other individuals, and in this sense, brood parasitism can be viewed as a female parallel to extra-pair mating in males (Petrie and Pike 2003). However, there are differences in the costs of such behavior. EPCs are costly only to males, whereas CBP is costly to both parasitized parents as both raise unrelated young (Rothstein and Robinson 1998).

Since CBP is costly to both parents, it may serve as an evolutionary selective force for the evolution of host defenses similar to those characteristic of the coevolutionary arms races between interspecific brood parasites and their hosts (Davis 2000). Host defenses against CBP may include a range of behavioral traits; however, the recognition and rejection of a parasitic egg are the most appropriate tactics documented mainly in interspecific parasitism (Rothstein and Robinson 1998). The recognition and rejection of conspecific eggs is supposed to be more difficult because of the similarity between the parasitic and host egg (Rothstein and Robinson 1998). Therefore, we performed a series of experiments with mimetic and non-mimetic eggs to evaluate the ability of the black-headed gull to respond to brood parasitism (Paper II).

The application of molecular techniques to avian mating systems has revealed striking variation in the incidence of alternative reproductive strategies, such as extra-pair paternity (EPP) and conspecific brood parasitism (CBP) (reviewed in Yom-Tov 1980, Yom-Tov 2001, Petrie and Møller 1991, Petrie and Kempenaers

1998). Understanding the factors, ecological, genetic or otherwise, that determine the prevalent mating system of a population is central to evolutionary biology, because it is the mating system that ultimately determines patterns of gene transmission across generations (Petrie et al. 1998). In light of the results from recent comparative studies, it seems that interspecific variation is determined prevalently by differences in life history and parental care, while variation between populations and individuals of the same species is more likely to be determined by differences in contemporary ecological and genetic factors (Arnold and Owens 2002). At the intraspecific level, the potential effect of some particular ecological factors was analyzed to estimate their influence on the probability of EPP and CBP rates in the black-headed gull (Paper II and III).

Paper I deals with primary sex ratio and sex ratio variation in the black-headed gull. Fisher (1930) theoretically explained why equal investment in sons and daughters should be an evolutionarily stable strategy. However, if the relative fitness of sons and daughters varies under different circumstances, it may be adaptive for parents to bias investment in favor of one sex (Trivers and Willard 1973, Charnov 1982).

Recently, there have been a number of reports documenting the ability of birds to facultatively manipulate the sex ratio of their offspring in response to a range of parental and environmental factors (Cluton-Brock 1986, Pike and Petrie 2003). Biased sex allocation has been reported when the reproductive value of sons and daughters varies, e.g. with: season (Dijkstra et al. 1990), habitat quality (Wiebe and Bortolotti 1992, Komdeur 1996), laying date (Fiala 1981, Daan et al. 1996, Korpimäki et al. 2000), laying order (Paper I, Müller et al. 2005), clutch size (Dijkstra et al. 1998),mate attractiveness (Ellegren et al. 1996, Sheldon et al. 1999), maternal age (Blank and Nolan 1983) and social status (Müller et al. 2002), maternal condition (Nager et al. 2000, Velando 2002, Pike and Petrie 2005), levels of maternal hormones (testosterone abd corticosterone, Pike and Petrie 2005, Pike and Petrie 2006).

The black-headed gull exhibits several life history traits that may influence sex ratio variation. First, the black-headed gull is a species with sexual size dimorphism, males being the larger sex. It has been hypothesized that larger body size makes males more vulnerable to adverse conditions because of their relative size and size-linked higher energy requirements (Nager et al. 1999, Kalmbach et al. 2001). Second, the hatching of black-headed gull chicks is asynchronous. Asynchrony and different rearing requirements for the sexes acting together could result in a strategy in which the sexes are hatched in some specific sequence (Bradbury and Griffiths 1999). In other words, this may lead to specific pattern of sex allocation in a clutch. Third, this pattern can be further modified by the timeing of breeding as a consequence of sex-differences in the survival and future reproductive prospects of chicks (Dijkstra et al. 1990).

REFERENCES

Alonso-Alvarez C 2006. Manipulation of primary sex ratio: an updated review. Avian and Polutry Biology Review 17: 1-20.

Alonso-Alvarez C, Velando A 2003. Female body condition and brood sex ratio in yellow-legged gulls *Larus cachinnans*. Ibis 145: 220-226.

Anderson DJ, Reeve J, Gomez JEM, Weathers WW, Huston S, Cunningham HV, Bird DM 1993. Sexual size dimorphism and food requirements of nestling birds. Canadian Journal of Zoology 71: 2541-2545.

Andersson M 1984. Brood parasitism within species. In: Producers and Scroungers: Strategies of Exploitation and Parasitism, pp. 195–228. Chapman and Hall, London.

Andersson M, Åhlund M 2000. Host-parasite relatedness shown by protein fingerprinting in a brood parasitic bird. Proceedings of the National Academy of Sciences USA 97: 13188– 13193.

Andersson M, Eriksson MOG 1982. Nest parasitism in goldeneyes *Bucephala clangula*: Some evolutionary aspects. American Naturalist 120: 1-16.

Appleby BM, Petty SJ, Blakey JK, Rainey P, MacDonald DW 1997. Does variation of sex ratio enhance reproductive success of offspring in tawny owls (Strix aluco)? Proceedings of Royal Society of London, series B 264: 1111-1116.

Arnold KE, Owens IPF 2002. Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation. Proceedings of Royal Society of London, series B 269: 1263-1269.

Badyaev AV, Schwabl H, Young RL, Duckworth RA, Navara KJ, Parlow AF 2005. Adaptive sex differences in growth of pre-ovulation oocytes in a passerine bird. Proceedings of Royal Society of London, series B 272: 2165-2172.

Bednarz JC, Hayden TJ 1991. Skewed brood sex ratio and sex-biased hatching sequence in Harris`s hawks. American Naturalist 137: 116-132.

Bennett PM, Owens IPF 2002. Evolutionary Ecology of Birds: Life Histories, Mating Systems and Extinction. Oxford University Press, Oxford.

Birkhead TR 1987. Behavioural adaptations to high density nesting in the common guillemot *Uria aalge*. Animal Behaviour 26: 321-331.

Birkhead TR, Møller AP 1992. Sperm Competition in Birds: Evolutionary Causes and Consequences. Academic Press, London.

Birkhead TR, Møller AP 1996. Monogamy and sperm competition in birds. In: Partnerships in Birds: the study of monogamy. Oxford University Press, Oxford, pp 323-343.

Birkhead TR, Møller AP 1998. Sperm Competition and Sexual Selection. Academic Press, London.

Bjørnstad G, Lifjeld JT 1997. High frequency of extra-pair paternity in a dense and synchronous population of willow warblers *Phylloscopus trochilus*. Journal of Avian Biology 8: 319-324.

Blanco G, Martínez-Padilla J, Dávila JA, Serrano D, Vinuela J 2003. First evidence of sex differences in the duration of avian embryonic period: consequences for sibling competition in sexually dimorphic birds. Behavioral Ecology 14: 702-706.

Blank JL, Nolan V 1983. Offspring sex ratio in red-winged blackbirds is dependent on maternal age. Proceedings of the National Academy of Science USA 80: 6141-6145.

Blount JD, Surai PF, Nager RG, Houston DC, Møller AP, Trewby ML, Kennedy MW 2002. Carotenoids and egg quality in the lesser black-backed gull *Larus fuscus*: a supplemental feeding study of maternal effects. Proceedings of Royal Society of London, series B 269: 29–36.

Bonnier F, Martin PR, Wingfield JC 2007. Maternal corticosteroids influence primary offspring sex ratio in a free-ranging passerine bird. Behavioral Ecology 18: 1045-1050.

Bradbury RB, Blakey JK 1998. Diet, maternal condition, and offspring sex ratio in the zebra finch, *Poephila guttata*. Proceedings of Royal Society of London, series B 265: 895-899.

Bradbury RB, 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.

Brown JL 1997. A theory of mate choice based on heterozygosity. Behavioral Ecology 8: 60-65.

Cézilly F, Nager RG 1995. Comparative evidence for a positive association between divorce and extra-pair paternity in birds. Proceedings of Royal Society of London, series B 262: 7-12.

Charnov EL 1982. The theory of sex allocation. Princeton University Press, Princeton.

Cichón M, Sendecka J, Gustafsson L 2005. Male-biased sex ratio among unhatched eggs in great tit *Parus major,* blue tit *P. caeruleus* and collared flycatcher *Ficedula albicollis*. Journal of Avian Biology 36: 386-390.

Clark AB 1978. Sex ratio and local resource competition in a prosimian primate. Science 201: 163-165.

Clout MN, Elliott GP, Robertson BC 2002. Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot. Biological Conservation 107: 13–18.

Clutton-Brock TH 1986. Sex ratio variation in birds. Ibis 128: 317-329.

Clutton-Brock TH 1991. The Evolution of Parental Care. Princeton University Press, Princeton.

Cockburn A, Legge S, Double MC 2002. Sex ratios in birds and mammals: can the hypotheses be disentangled? In: Sex ratios. Concepts and research methods. Cambridge University Press, Cambridge, pp 265-286.

Cook MI, Monaghan P 2004. Sex differences in embryo development periods and effects on avian hatching patterns. Behavioral Ecology 15: 205-209.

Correa SM, Adkins-Regan E, Johnson PA 2005. High progesterone during avian meiosis biases sex ratio toward females. Biological Letters 1: 215-218.

Daan S, Dijkstra C, Weissing FJ 1996. An evolutionary explanation for seasonal trends in avian sex ratios. Behavioral Ecology7: 426-430.

Davies NB 2000. Cuckoo, cowbirds and the other cheaters. Poyser, London.

Decoux JP 1997. Variation de la sex-ratio secondaire chez les oiseaux et autres tétrapodes le cas de *Colius striatus nigricollis* (Coliiformes). Revue d'Ecologie – la Terre et la Vie 52: 37-68.

Dickinson JL 2007. Decoding dumping ducks. Molecular Ecology 16: 2610-2612.

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

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

Dugger BD, Blums P 2001. Effect of conspecific brood parasitism on host fitness for tufted duck and common pochard. Auk 118: 717-726.

Eadie JMcA, Kehoe FP, Nudds TD 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. Canadian Journal of Zoology 66: 1709– 1721.

Ellegren H, Gustafsson l, Sheldon BC 1996. Sex ratio adjustment in relation to parental attractiveness in a wild bird population. Proceedings of the National Academy of Science USA 93: 11723-11728.

Ellegren H, Sheldon BC 1997. New tools for sex identification and the study of sex allocation in birds. Trends in Ecology and Evolution 12: 255-259.

Elmen ST 1997. When mothers prefer daughters over sons. Trends in Ecology and Evolution 12: 291-292.

Fiala KL 1981. Sex Ratio Constancy in the red-winged blackbird. Evolution 35: 898-910.

Fisher RA 1930. The genetical theory of natural selection. Clarendon Press, Oxford.

Frank SA 1990. Sex allocation theory for birds and mammals. Annual Revue of Ecology and Systematics 21: 13–55.

Gasparini J, McCoy KD, Haussy C, Tveraa T, Boulinier T 2001. Induced maternal response to the Lyme disease sprirochaete *Borrelia burgdorferi sensu lato* in a colonial seabird, the kittiwake *Rissa tridactyla.* Proceedings of Royal Society of London, series B 268: 1-4.

Geffen E, Yom-Tov Y 2001. Factors affecting the rates of intraspecific nest parasitism among Anseriformes and Galliformes. Animal Behaviour 62: 1027-1038.

Gowaty P A 1991. Facultative manipulation of sex ratios in bird. Rare or rarely observed ? Current Ornithology 8: 141–170.

Gowaty PA 1993. Differential dispersal, local resource competition, and sex-ratio variation in birds. American Naturalist 141: 263-280.

Gowaty PA 1996. Battles of the sexes and origins of monogamy. In: Partnerships in Birds: the study of monogamy. Oxford University Press, Oxford, pp 21-52.

Gowaty PA, Lennartz MR 1985. Sex ratio of nestling and fledgling red-cockaded woodpeckers (*Picoides borealis*) favor males. American Naturalist 126: 347-353.

Gray EM 1997. Female red-winged blackbirds accrue material benefits from copulating with extra-pair males. Animal Behaviour 53: 625-639.

Griffith SC, Örnborg J, RussellL AF, Andersson S, Sheldon BC 2003. Correlations between ultraviolet coloration, overwinter survival and offspring sex ratio in the blue tit. Journal of Evolutionary Biology 16: 1045–1054.

Griffith SC, Owens IPF, Thuman KA 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Molecular Ecology 11: 2195-2212.

Griffiths R, Double MC, Orr K, Dawson RJG 1998. A DNA test to sex most birds. Molecular Ecology 7: 1071–1075.

Hamilton WD 1967. Extraordinary sex ratios. Science 1565: 477-478.

Hardy IC 2002. Sex ratios. Concepts and research methods. Cambridge University Press, Cambridge.

Hasselquist D, Bensch S, Vonschantz T 1995. Low-frequency of extra-pair paternity in the polygynous great reed warbler *Acrocephalus arundinaceus*. Behavioral Ecology 6: 27-38.

Hasselquist D, Kempenaers B 2002. Parental care and adaptive brood sex ratio manipulation in birds. Philosophical Transactions in the Royal Society of London, series B 357: 363–372.

Heinsohn R, Legge S, Barry S 1997. Extreme bias in sex allocation in Eclectus parrots. Proceedings of Royal Society of London, series B 264: 1325-1329.

Hepp GR, Kennamer RA, Harvey WF 1990. Incubation as a reproductive cost in female ducks. Auk 107: 756-764.

Hoi H, Hoi-Leitner M 1997. An alternative route to coloniality in the bearded tit: Females pursue extra-pair fertilizations. Behavioral Ecology 8: 113-119.

Howe HF 1977. Sex-Ratio Adjustment in the Common Grackle. Science 198: 744-746.

Jackson WM 1998. Egg discrimination and egg color variability in the northern masked weaver: the importance of conspecific versus interspecific parasitism. In: Parasitic Birds and Their Hosts: Studies in Coevolution. Oxford University Press, Oxford, pp 407-418.

Johnson AL 2000. Reproduction in female. In: Sturkie´s Avian Physiology. Academic Press, London, pp 569-596.

Julliard R 2000. Sex-specific dispersal in spatially varying environments leads to habitat-dependent evolutionarily stable offspring sex ratios. Behavioral Ecology 11: 421-428.

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

Kempenaers B, Congdon B, Boag P, Robertson RJ 1999. Extrapair paternity and egg hatchability in tree swallows: evidence for genetic compatibility hypothesis? Behavioral Ecology 10: 304-311.

Kilner R 1998. Primary and secondary sex ratio manipulation by zebra finches. Animal Behaviour 56: 155–164.

Koenig WD, Stanback MT, Haydock J, Kraaijeveld-Smit F 2001. Nestling sex ratio variation in the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*). Behavioural Ecology and Sociobiology 49:357–365.

Kölliker M, Heeb P, Werner I, Mateman AC, Lessells CM, Richner H 1999. Offspring sex ratio is related to male body size in the great tit (*Parus major*). Behavioral Ecology 10: 68-72.

Komdeur J 1994. Experimental evidence for helping and hindering by previous offspring in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*). Behavioral Ecology and Sociobiology 4: 31–42.

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

Komdeur J 1998. Long-term fitness benefits of egg sex modification by the Seychelles warbler. Ecological Letters 1: 56–62.

Komdeur J, Daan S, Tinbergen J, Mateman Ch 1997. Extreme adaptive modification in sex ratio of the Seychelles warbler´s eggs. Nature 385: 522-526.

Komdeur J, Magrath MJL, Krackow S 2002. Pre-ovulation control of hatchling sex ratio in the Seychelles warbler. Proceedings of Royal Society of London, series B 269: 1067-1072.

Komdeur J, Pen I 2002. Adaptive sex allocation in birds: the complexities of linking theory and practice. Philosophical Transactions in the Royal Society of London, series B 357: 373–380.

Korpimaki E, May CA, Parkin DT, Wetton JH, Wiehn J 2000. Enviromental- and parental condition-related variation in sex ratio of kestrel broods. Journal of Avian Biology 31: 128-134.

Krackow S 1995. Potential mechanism for sex ratio adjustment in mammals and birds. Biological Review 70: 225-241.

Krackow S 1999. Avian sex ratio distortions: The myth of maternal control. In: Proceedings of 22 International Ornithological Congress, Durban (eds. Adams NJ, Slotow RH), pp 425-433. Johannesburg: BirdLife South Africa.

Krebs EA, Green DJ, Double MC, Griffiths R 2002. Laying date and laying sequence influence the sex ratio of crimson rosella broods. Behavioral Ecology and Sociobiology 51: 447-454.

Krijgsveld K, Dijkstra C, Visser GH, Daan S 1998. Energy requirements for growth in relation to sexual size dimorphism in marsh harrier *Circus aeruginosus* nestlings. Physiological Zoology 71: 693–702.

Legge S, Heinsohn R, Double MC, Griffiths R, Cockburn A 2001. Complex sex allocation in the laughing kookaburra. Behavioral Ecology 12: 524 – 533.

Lessells CM, Mateman AC, Visser J 1996. Great tit hatchling sex ratios. Journal of Avian Biology 27: 135-142.

Ležalová R, Tkadlec E, Oborník M, Šimek J, Honza M 2005. Should males come first? The relationship between offspring hatching order and sex in the black-headed gull *Larus ridibundus*. Journal of Avian Biology 36: 478-483.

Ligon JD, Ligon SH 1990. Female-biased sex ratio at hatching in the green woodhoopoe. Auk 107: 765–771

López-Sepulcre A, Kokko H 2002. The role of kin recognition in the evolution of conspecific brood parasitism. Animal Behaviour 64: 215-222.

Mauck RA, Marschal EA, Parker PG 1999. Adult survival and imperfect assessment of parentage : Effects on male parenting decisions. American Naturalist 142:118-140.

Møller AP 1998. Density-dependent intraspecific nest parasitism and anti-parasite behavior in the barn swallow *Hirundo rustica*. In: Parasitic Birds and Their Hosts: Studies in Coevolution. Oxford University Press, Oxford, pp 396-406.

Møller AP, Ninni P 1998. Sperm competition and sexual selection: a meta analysis of paternity studies of birds. Behavioral Ecology and Sociobiology 43: 345-358.

Müller W, Eising CM, Dijkstra C, Groothuis TGG 2002. Sex differences in yolk hormones depend on maternal social status in Leghorn chickens (*Gallus gallus domesticus*). Proceedings of Royal Society of London, series B 269: 2249-2255.

Myers JH 1978. Sex ratio adjustment under food stress: Maximization of quality or numbers of offspring? American Naturalist 112: 381-388.

Nager RG, Monaghan P, Griffiths R, Houston DC, Dawson R 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. Proceedings of the National Academy of Science USA 96: 570-573.

Nager RG, Monaghan P, Houston DC 2000. Within-clutch trade-offs between the number and quality of eggs: experimental manipulations in gulls. Ecology 81: 1339-1350.

Neudorf DLH 2004. Extrapair paternty in birds: understanding variation among species. Auk 121: 302-307.

Nielsen CR, Parker PG, Gates RJ 2006. Intraspecific nest parasitism of cavity-nesting wood ducks: costs and benefits to hosts and parasites. Animal Behaviour 72: 917-926.

Nishiumi I 1998. Brood sex ratio is dependent on female mating status in polygynous great reed warblers. Behavioral Ecology and Sociobiology 44: 9-14.

Nishiumi I, Yamagishi S, Maekawa H, Shimoda C 1996. Paternal expenditure is related to brood sex ratio in polygynous great reed warblers. Behavioral Ecology and Sociobiology 39: 211–217.

Oddie KR 1998. Sex discrimination before birth. Trends in Ecology and Evolution 13: 130-131.

Oddie KR 2000. Size matters: competition between male and female great tit offspring. Journal of Animal Ecology 69: 903-912.

Payne RB 1977. The ecology of brood parasitism in birds. Annual Revue in Ecology and Systematics 8: 1-28.

Petrie M, Kempenaers B 1998. Extra-pair paternity in birds: explaining variation between species and populations. Trends in Ecology and Evolution 13: 52-58.

Petrie M, Møller AP 1991. Laying eggs in others' nests: Intraspecific brood parasitism in birds. Trends in Ecology and Evolution 6: 315-320.

Petrie M, Schwabl H, Brande-Lavridsen N, Burke T 2001. Sex differences in avian yolk hormone levels. Nature 412: 498.

Pike TW 2005. Sex ratio manipulation in response to maternal condition in pigeons: evidence for pre-ovulatory follicle selection. Behavioral Ecology and Sociobiology 58: 407–413.

Pike WP, Petrie M 2003. Potential mechanism of avian sex manipulation. Biological Review 78: 553-574.

Pike TW, Petrie M 2005. Maternal body condition and plasma hormones affect offspring sex ratio in peafowl. Animal Behaviour 70: 745–751.

Pike TW, Petrie M 2006. Experimental evidence that corticosterone affects offspring sex ratios in quail. Proceedings of Royal Society of London, series B 273: 1093–1098.

Rathburn MK, Montgomerie R 2004. Offspring sex ratios correlate with pair–male condition in a cooperatively breeding fairy–wren. Behavioral Ecology 16: 41-47.

Rohwer FC, Freeman S 1989. The distribution of conspecific nest parasitism in birds. Canadian Journal of Zoology 67: 239-253.

Rothstein SI, Robinson SK 1998. Parasitic Birds and Their Hosts: Studies in Coevolution. Oxford University Press, Oxford.

Royle NJ, Surai PF, McCartney RJ, Speake BK 1999. Parental investment and egg yolk lipid composition in gulls. Functional Ecology 13: 298-306.

Rutkowska J, Cichón M 2006. Maternal testosterone affects the primary sex ratio and offspring survival in zebra finches. Animal Behaviour 71: 1283-1288.

Rutstein AN, Gilbert L, Slater PJB, Graves JA 2004. Mate attractiveness and primary resource allocation in the zebra finch. Animal Behaviour 68: 1087-1094.

Ryder JP 1983. Sex ratio and egg sequence in ring-billed gulls. Auk 100: 726-729.

Salomons HM, Müller W, Dijkstra C, Eising CM, Verhulst S 2006. No sexual differences in embryonic period in jackdaws *Corvus monedula* and black-headed gulls *Larus ridibundus*. Journal of Avian Biology 37: 19-22.

Schwabl H 1993. Yolk is a source of maternal testosterone for developing birds. Proceedings of the National Academy of Science USA 90: 11446-11450.

Semel B, Sherman PW 2001. Intraspecific parasitism and nest site competition in wood ducks. Animal Behaviour 61: 787–803.

Sheldon BC 1998. Recent studies of avian sex ratio: Short review. Heredity 80: 397- 402.

Sheldon BC, Andersson S, Griffith SC, Örnborg J, Sendecka J 1999. Ultraviolet colour variation influences blue tit sex ratios. Nature 402: 874-877.

Sheldon BC, Merilä J, Qvarnström L, Gustafsson L, Ellegren H 1997. Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. Proceedings of Royal Society of London, series B 264: 297-302.

Smallwood PD, Smallwood JA 1998. Seasonal shifts in sex ratios of fledgling American kestrels (*Falco sparverius paulus*): The early bird hypothesis. Evolutionary Ecology 12: 839-853.

Sorenson MD 1991. The functional significance of parasitic egg laying and typical nesting in redhead ducks: an analysis of individual behaviour. Animal Behaviour 42: 771-796.

Sorenson MD 1992. Comment: Why is conspecific nest parasitism more frequent in waterfowl than in other birds? Canadian Journal of Zoology 90: 1856-1858.

Sorenson MD 1997. Effects of intra- and interspecific brood parasitism on a precocial host, the canvasback, *Aythya valisineria*. Behavioral Ecology 8: 155-161.

Sorenson MD 1998. Patterns of parasitic egg laying and typical nesting in redhead and canvasback ducks. In: Parasitic Birds and Their Hosts: Studies in Coevolution. Oxford University Press, Oxford, pp 537-375.

Sturkie PD 2000. Sturkie´s Avian Physiology, 5th edition. Academic Press, San Diego.

Stutchbury BJ, Morton ES 1995. The effect of breeding synchrony on extra-pair mating system in songbirds. Behaviour 132: 675–90.

Svensson E, Nilsson JA 1996. Mate quality affects offspring sex ratio in blue tits. Proceedings of Royal Society of London, series B 263: 357-361.

Tella JL, Donazar JA, Negro JJ, Hiraldo F 1996. Seasonal and interannual variations in the sex-ratio of lesser kestrel *Falco naumanni* broods. Ibis 138: 342-345.

Thomson DL, Monaghan P, Furness RW 1998. The demands of incubation and avian clutch size. Biological Reviews 73: 293-304.

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

Trivers RL 1972. Parental investment and sexual selection. In: Sexual selection and the descent of man. Heineman, London.

Trivers RL, Willard DE 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179: 90–92.

Veiga JP, Vinuela J, Cordero PJ, Aparicio JM, Polo V 2004. Experimentally increased testosterone affects social rank and primary sex ratio in the spotless starling. Hormones and Behavior 46: 47-53.

Velando A 2002. Experimental manipulation of maternal effort produces differential effects in sons and daughters: implications for adaptive sex ratios in the blue-footed booby. Behavioral Ecology 13: 443–449.

Wagner RH 1992. The pursuit of extra-pair copulations by monogamous female razorbills: how do females benefit? Behavioral Ecology and Sociobiology 29: 455-464.

Weimerskirch H, Lallemand J, Martin J 2005. Population sex ratio variation in a monogamous long-lived bird, the wandering albatross. Journal of Animal Ecology 74: 285–291.

Westerdahl H, Bensch S, Hansson B, Hasselquist D, von Schantz T 1997. Sex ratio variation among broods of great reed warblers *Acrocephalus arundinaceus*. Molecular Ecology 6: 543-548.

Westerdahl H, Bensch S, Hansson B, Hasselquist D, von Schantz T 2000. Brood sex ratios, female harem status and resources for nestling provisioning in the great reed warbler (*Acrocephalus arundinaceus*). Behavioral Ecology and Sociobiology 47: 312-318.

Westneat DF, Sargent RC 1996. Sex and parenting – the effects of sexual conflict and parentage on parental strategies. Trends in Ecology and Evolution 11: 87-91.

Westneat DF, Sherman PW 1997. Density and extra-pair fertilizations in birds: a comparative analysis. Behavioral Ecology and Sociobiology 41: 205-215.

Westneat DF, Sherman PW, Morton ML 1990. The ecology and evolution of extra pair copulations in birds. Current Ornithology 7: 331-369.

Whittingham LA, Dunn PO, Nooker JK 2005. Maternal influences on brood sex ratios: an experimental study in tree swallows. Proceedings of Royal Society of London, series B 272: 1775-1780.

Wiebe KL, Bortolotti GR 1992. Facultative sex-ratio manipulation in American kestrels. Behavioral Ecology and Sociobiology 30: 379-386.

Yezerinac SM, Gibbs HL, Briskie JV, Whittam R, Montgomerie R 1999. Extrapair paternity in a far northern population of yellow warblers *Dendroica petechia*. Journal of Avian Biology 30: 234-237.

Yom-Tov Y 1980. Intraspecific nest parasitism in birds. Biological Review 55: 93-108.

Yom-Tov Y 2001. An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. Ibis 143: 133-143.

Zijlstra M, Daan S, Bruinenberg-Rinsma J 1992. Seasonal variation in the sex ratio of marsh harrier *Circus aeruginosus* broods. Functional Ecology 6: 553-559.

Zink AG 2000. The evolution of intraspecific brood parasitism in birds and insects. American Naturalist 155: 395-405.

Ležalová Radka, Tkadlec Emil, Oborník Miroslav, Šimek Jaroslav, Honza Marcel

Should males come first? The relationship between offspring hatching order and sex in the black-headed gull *Larus ridibundus.*

Journal of Avian Biology 36: 478 – 483, 2005.

Radka Ležalová: Department of Zoology, Faculty of Biological Sciences, and Laboratory of Molecular Taxonomy, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic.
Emil Tkadlec: Palacky University, Department of Ecology & Environmental Sciences, tr. Svobody 26, Olomouc, 77146.
Miroslav Oborník: Laboratory of Molecular Taxonomy, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic.
Jaroslav Šimek: Department of Zoology, Faculty of Biological Sciences University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic.
Marcel Honza: Institute of Vertebrate Biology Academy of Sciences of the Czech Republic, Květná 8, 603 65 Brno, Czech Republic.

ABSTRACT

In birds with hatching asynchrony and sexual size dimorphism, chicks hatched earlier and later in the laying sequence usually suffer different mortalities due to uneven abilities to compete for food, especially in poor years. If sexes differ in vulnerability to environmental conditions, e.g., by having different food requirements due to differential growth rates, mothers can increase fitness by allocating sex according to the laying order, producing less vulnerable sex later rather than early in the clutch. By analysing variation in primary sex ratio using a PCR-based DNA technique, we tested this prediction in black-headed gull *Larus ridibundus* chicks where males may be the less viable sex under adverse conditions. The overall primary sex ratio of the population did not depart from parity. However, first hatched chicks were more likely to be males whereas last hatched chicks were more likely to be females. Both egg volume and hatchling body mass decreased with laying order irrespective of sex. Time of breeding had no effect on offspring sex or hatchling sex ratios .

ABSTRAKT

U velikostně dimorfních druhů ptáků, kde dochází k asynchronímu líhnutí mláďat jsou mláďata líhnoucí se z prvních a posledních vajec ve snůšce postižena rozdílnou mírou mortality v důsledku nestejné schopnosti kompetice o potravu a to především v období nedostatku potravy. Jestliže je jedno pohlaví náchylnější na změny okolního prostředí a následkem toho má vyšší nároky na rodičovskou péči, pak samice může pomocí specifické alokace pohlaví mláďat s ohledem na jejich pořadí ve snůšce ovlivnit jejich fitness tak, že produkuje to životaschopnější pohlaví ve snůšce později. Pomocí analýzy variance primárního poměru pohlaví jsme testovali tyto předpoklady u racka chechtavého (Larus ridibundus), kde za nepříznivých podmínek jsou samci tím méně životaschopným pohlavím.

Celkově se primární poměr pohlaví mláďat v populaci nelišil od rovnováhy. Ale mláďata která se ve snůšce líhla jako první byla s velkou pravděpodobností samčího pohlaví, zatímco třetí mláďata byla převážně pohlaví samičího. Objem vejce a váha líhnoucích se mláďat klesala s pořadím ve snůšce nezávisle na pohlaví. Nebyl zjištěn žádný vliv načasování hnízdění na pohlaví mláďat.

Ležalová-Piálková Radka, Honza Marcel

Responses of Black-headed Gulls *Larus ridibundus* to conspecific brood parasitism.

Journal of Ornithology 149: 415-42, 2008.

Ležalová-Piálková Radka: Institute of Vertebrate Biology Academy of Sciences of the Czech Republic, Květná 8, 60365 Brno, Czech Republic.
Department of Zoology, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, 37005 České Budějovice, Czech Republic.
Honza Marcel: Institute of Vertebrate Biology Academy of Sciences of the Czech Republic, Květná 8, 60365 Brno, Czech Republic.

ABSTRACT

Conspecific brood parasitism in birds occurs when a female inserts her egg into the clutch of her own species. If successful, i.e. the parasitic egg is accepted by the host, then the host female or pair rears the offspring of the parasite. In the present study, we studied natural conspecific brood parasitism in black-headed gulls (*Larus ridibundus*), and conducted series of the experiments with mimetic (conspecific) and non-mimetic (conspecific painted light blue) eggs to explore responses of the tested pairs towards these alien eggs. The natural parasitism rate was 10% and the probability of being parasitized significantly increased with nest density. Experimentally parasitized pairs rejected both types of experimental eggs at a similar rate - 14.3 % for mimetic and 25.5% for, non-mimetic within two days. Non-mimetic eggs were more selectively rejected than mimetic eggs. The relationships between the probability of egg rejection (dependent variable) and predictor (independent) variables were examined by fitting generalized linear models. Contrast and intraclutch variation in ground color and spotting pattern, and the volume of the egg had no significant effect on rejection behavior in either non-mimetic or mimetic eggs. However, nest density significantly positively affected rejection behavior of the black-headed gull, in both non-mimetic and mimetic treatments.

ABSTRAKT

K vnitrodruhovému hnízdnímu parazitizmu ptáků dochází, když samice snáší svá vejce do hnízd jiných samic svého druhu. V případě, že je parazitické vejce hostiteli přijato, potom hostitelé přebírají péči o mládě parazita. V této práci jsme studovali frekvenci vnitrodruhového hnízdního parazitizmu u racka chechtavého (*Larus ridibundus*) a déle pomocí série experimentů s mimetickými a nemimetickými vajíčky testovali reakci hostitelského páru na přítomnost parazitického vajíčka ve snůšce. Zjištěná frekvence vnitrodruhového hnízdní parazitizmu byla 10% a pravděpodobnost, že k parazitaci v určitém hnízdě dojde, se signifikantně zvyšovala s rostoucí hustotou hnízd v kolonii. Experimentálně parazitované páry byly schopny odmítnout oba typy experimentálních parazitických vajec s přibližně stejnou frekvencí – 14.3% v případě mimetických vajec a 25.5% v případě nemimetických vajec. Nemimetická vejce byla odstraňována s větší selektivitou než vejce mimetická. Pomocí zobecněných lineárních modelů byla testována pravděpodobnost odmítnutí parazitického vejce v závislosti na vybraných faktorech. Kontrast a vnitrodruhová variabilita ve zbarvení a skvrnitosti vajec a objem vejce neměli vliv na odmítnutí ani nemimetických ani mimetických vajec. Významný pozitivní vliv na toto chování měla pouze hustota hnízd v rámci kolonie a to v případě obou typů vajec.

Ležalová-Piálková Radka

Molecular evidence for extra-pair paternity and intraspecific brood parasitism in Black-headed Gull.

submitted

Ležalová-Piálková Radka: Institute of Vertebrate Biology Academy of Sciences of the Czech Republic, Květná 8, 60365 Brno, Czech Republic.
Department of Zoology, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, 37005 České Budějovice, Czech Republic.

ABSTRACT

Social monogamy is common among birds, while genetic monogamy is supposed to be rare. I investigated the genetic mating system of the Black-headed Gull *Larus ridibundus*, where, as in seabirds and most other long-lived and socially monogamous birds, extra-pair paternity (EPP) is typically rather infrequent. Parentage was determined using six microsatellite markers for 79 chicks from 30 broods. In this study population, I found evidence of allelic inconsistencies between putative parents and chicks in 43% of nests, resulting from both EPP and intraspecific brood parasitism (ISBP). Extra-pair paternity was detected in 33 % (10/30) of broods, and 20% (16/79) of all nestlings were sired by extra-pair males. Furthermore, 9% (7/79) of chicks out of 5 nests (17%) were not the offspring of either member of the pair, indicating ISBP. The probability of an extra-pair young in a nest increased significantly with colony nest density in the colony and average egg volume in the clutch, but this was not observed for ISBP. These findings reveal a moderate rate of ISBP and a high rate of EPP compared with other related species, and shows that Black-headed Gulls successfully participate in extra-pair copulations.

Abstrakt

Zatímco sociální monogamie je mezi ptáky běžná, genetická monogamie je poměrně vzácná. Studovala jsem genetický pářicí systém racka chechtavého (Larus ridibundus), u kterého se předpokládá, že podobně jako u většiny dlouhověkých, sociálně monogamních ptačích druhů, dochází k mimo-párovým paternitám (EPP) a vnitrodruhovému hnízdnímu parazitizmu (ISBP) velmi zřídka. Genetické vztahy uvnitř 30 rodin (79 mláďat) byly studovány pomocí analýzy šesti mikrosatelitů. Ve 43% hnízd byly nalezeny nesrovnalosti mezi alelami rodičů a mláďat, které byly důsledkem jak EPP, tak i ISBP. Mimo-párová paternita byla detekována ve 33% hnízd (10/30) a 20% (16/79) mláďat ze studované populace bylo mimo-párových a dále 9% (7/79) mláďat pocházejících z pěti hnízd (17%) bylo parazitických. Pravděpodobnost výskytu mimo-párového mláděte ve hnízdě signifikantně vzrůstá s hustotou hnízd na kolonii a průměrným objemem vajec ve snůšce. V případě ISBP tento trend zjištěn nebyl.

ACKNOWLEDGEMENTS

Ze všeho nejvíce bych chtěla poděkovat svým rodičům za to, že mně umožnili pěstovat zálibu z jejich pohledu značně obskurní, to jest ornitologii. Ba co víc, ještě mě v této činnosti tak dlouho podporovali.

During my studies many persons have helped and influenced me at various ways. I am grateful to be surrounded by people at Faculty of Sciences, not only from Department of Zoology, which create such pleasant and family atmosphere during my study. Firstly, my thanks go to Jaroslav Šimek, who initiated me to study gulls and withstanded to supervise me for six years. I am also obligate to Roman Fuchs agreeing to be the guarantee of my PhD thesis.

My other thanks belong to Miroslav Oborník who introduced me to the molecular word and enabled me to work in his Laboratory of Molecular Taxonomy of PrF JU, which I truly appreciate.

My special thanks go to Marcel Honza for all his contributions to this thesis, namely invaluable help in field. For the nice and stimulating atmosphere during the field work at “Bojanovice” I want to express my gratitude also to other colleagues from Department of Avian Ecology of ASCR in Brno (Petr Procházka, Milica Požgayová, Lenka Poláčiková, to mention a few).

I am also very grateful to David Hardekopf for reading the thesis throughout and correcting what I thought to be English.

Finally, I would like to thank my friends (namely to Roman Hrdlička and Pavla Robovská) and all my family, especially to Luboš and Vašek for their endless support and patience.

Department of Zoology
Faculty of Science
University of South Bohemia

Department of Avian Ecology
Institute of Vertebrate Biology
Academy of Science of the Czech Republic