



Effect of food availability on offspring sex ratios in replacement clutches of Mew Gulls (*Larus canus*) and Black-headed Gulls (*Chroicocephalus ridibundus*) in the highly unstable environment of the Vistula River

Dariusz Bukaciński¹ · Monika Bukacińska¹ · Przemysław Chylarecki²

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Abstract

The reproductive cost hypothesis predicts that parents with low investment capacity (e.g., those in poor condition) should produce the larger sex (usually males) less often so as to minimize the risk of current reproductive failure and/or a decrease in their residual reproductive value. The study aimed to test whether offspring sex ratio bias in replacement clutches of the Mew Gull (MG; *Larus canus*) and Black-headed Gull (BHG; *Chroicocephalus ridibundus*) exposed to different food conditions was in agreement with predictions of the reproductive cost hypothesis. Food availability was experimentally modified before egg laying. Our experimental treatment affected hatching sex ratio, being also significant the effect of laying order and species identity. For both gull species, parents that were provided with supplemental food had more sons at hatching than unfed (control) pairs. This was particularly so if they were fed until production of a replacement clutch. This gradient in hatching sex ratio was much more pronounced in MG than in BHG. In both gull species, sons hatched more often from first laid (A) than from second (B) or third-laid egg (C). Five days after hatching, the sex ratio of surviving chicks was dependent mainly on the experimental treatment and egg sequence. Unlike the time of hatching, there was no important effect of species × treatment interaction. In both gull species, the brood sex-ratio was clearly male-biased in parents receiving supplemental feeding. However, differences between experimental groups were less extreme than at hatching. Chicks hatched from C-egg had much lower survival than chicks from the first two eggs (A- and B-egg), irrespective of sex, treatment, or species. Supplementary feeding was associated with improved chick survival for both gull species, although this effect was dependent on chick gender. Surprisingly, in the case of control broods (i.e., broods whose parents did not receive supplementary food), male chicks survived better than female chicks, but the opposite was true for broods in which parents were fed. There was an overall tendency for higher survival of BHG chicks than MG chicks. During the early-chick period, competition between siblings and the related differentiated mortality of chicks from A-, B-, and C-eggs, constituted a mechanism which shaped the brood sex ratio bias. In this context, differences in the sex ratio bias in eggs of different rank (A, B, C) at hatching were important. The results appear to fulfil the expectations of the reproductive cost hypothesis. For the species with greater sexual dimorphism (MG), a relationship between the condition of parents and the expected bias of sex ratio was visible only at hatching, which may indicate that this feature is not significant in shaping the sex ratio bias in MG.

Keywords Black-headed gull · Food availability · Mew gull · Offspring sex ratios · Replacement clutches · Sexual size dimorphism

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✉ Dariusz Bukaciński
dbukacinski@op.pl

Extended author information available on the last page of the article

Zusammenfassung

Auswirkung des Futterangebotes auf das Geschlechterverhältnis bei Jungen in Nachgelegen von Sturmmöwen (*Larus canus*) und Lachmöwen (*Chroicocephalus ridibundus*) in einem hochgradig instabilen Ökosystem an der Weichsel

Die Reproduktionskosten-Hypothese besagt, dass Elterntiere mit geringen Investitionsmöglichkeiten (z.B. wegen eines schlechten Gesamtzustands) weniger häufig Nachkommen des größeren Geschlechts (normalerweise Männchen) zeugen, um das Risiko eines Fortpflanzungsausfalls oder einer Verringerung ihres Rest-Fortpflanzungswertes so gering wie möglich zu halten. Unsere Untersuchung sollte feststellen, ob das Geschlechterverhältnis der Jungen in Nachgelegen von Sturmmöwen (*Larus canus*) und Lachmöwen (*Chroicocephalus ridibundus*), die unterschiedliche Futterangebote erhielten, mit den Vorhersagen der Reproduktionskosten-Hypothese in Übereinklang stand. Das Futterangebot wurde vor der Eiablage verändert. Unsere Versuche beeinflussten in der Tat das Geschlechterverhältnis der Geschlüpften sowie in signifikanter Weise auch die Reihenfolge der Eiablage. Bei beiden Möwenarten hatten diejenigen Eltern, die zusätzliches Futter erhielten, mehr geschlüpfte Söhne als die nicht zusätzlich gefütterten (Kontroll-)Paare. Dies galt vor allem, wenn sie bis zur Ablage eines Nachgeleges gefüttert wurden. Der Gradient im Geschlechterverhältnis der frisch Geschlüpften war bei den Sturmmöwen stärker ausgeprägt als bei den Lachmöwen. Bei beiden Möwenarten gab es bei den erstgelegten Eiern (A) mehr Söhne als bei den zweit- (B) oder drittgelegten (C). Fünf Tage nach dem Schlüpfen hing das Geschlechterverhältnis der überlebenden Küken in erster Linie von der experimentellen Behandlung und von der Reihenfolge der gelegten Eier ab. Abgesehen vom Zeitpunkt des Schlüpfens konnten keine wichtigen Effekte im Zusammenhang zwischen Möwenart und experimenteller Behandlung festgestellt werden. Bei beiden Möwenarten gab es ein klares Übergewicht an männlichen Jungen bei den Eltern mit zusätzlichem Futter. Aber die Unterschiede zwischen allen Gruppen des Experiments waren weniger groß als beim Schlüpfen. Küken aus C-Eiern zeigten unabhängig von Geschlecht, Behandlung oder Spezies eine viel kleinere Überlebensrate als solche aus den ersten zwei gelegten Eiern (A und B). Bei beiden Möwenarten war die zusätzliche Fütterung mit einer höheren Überlebensrate verbunden, wobei dieser Effekt jedoch vom Geschlecht der Küken abhing. Überraschenderweise überlebten in den Kontrollbruten (deren Eltern kein zusätzliches Futter erhielten) mehr männliche als weibliche Küken, aber in den Gruppen mit zusätzlichem Futter war es umgekehrt. Die Küken der Lachmöwen zeigten tendenziell eine höhere Überlebensrate als die der Sturmmöwen. Während der ersten Zeit nach dem Schlüpfen bildete die Konkurrenz zwischen den Geschwistern und die unterschiedliche Sterberate der Küken aus A-, B- und C-Eiern eine Art Mechanismus, aus dem sich das Geschlechterverhältnis in den Bruten ergab. In diesem Zusammenhang gewannen die Unterschiede in den Geschlechterverhältnissen der Jungen aus A-, B- und C-Eiern an Bedeutung. Diese Ergebnisse scheinen die Erwartungen aus der Reproduktionskosten-Hypothese zu erfüllen. Für die Art mit dem größeren Geschlechtsdimorphismus (Sturmmöwen) gab es nur beim Schlüpfen einen Zusammenhang zwischen der Gesamtverfassung der Eltern und dem zu erwartenden Geschlechterverhältnis, was nahelegt, dass dieses Merkmal bei Sturmmöwen nicht wichtig für das Zustandekommen des Geschlechterverhältnisses ist.

Introduction

Sex allocation theory predicts that parents should adjust the sex ratio of their offspring according to the costs and benefits related to the production of one or the other sex in a given context (Charnov 1982; Frank 1990; West 2009). Several hypotheses have been proposed that focus on the different selection pressures that could potentially influence sex ratio adjustment in birds and mammals (reviewed in Cockburn et al. 2002). Although an adaptive sex ratio bias among offspring has been shown in a large number of studies (as reviewed in Alonso-Alvarez 2006; Komdeur 2012), the results are often inconsistent, even within the same species (Rosivall et al. 2004; Maddox and Weatherhead 2009; Merklings et al. 2015 vs. 2019). Other studies reported only a small sex ratio bias (Torres and Drummond 1999; Weimerskirch and Lys 2000; Boulet et al. 2001), lack of sex ratio bias, or even bias in the opposite direction than that predicted by models (Leech et al. 2001; Cockburn and Double 2008;

Oddie and Reim 2002; Kalmbach et al. 2005). This may reflect the fact that factors shaping the sex ratio are much more complex than those acknowledged in the most widely used sex allocation models.

Two of the most popular models of sex allocation—the reproductive cost hypothesis (Myers 1978; Cockburn et al. 2002) and the Trivers–Willard hypothesis (Trivers and Willard 1973)—focus on parental condition as a driver of observed variation in offspring sex ratio. They both predict that in species, where males are larger, females in poor condition should overproduce daughters, although such hypotheses differ regarding the postulated mechanisms (fitness return pathways, sensu Merklings et al. 2015) leading to such a bias. In birds with male-biased sexual size dimorphism, raising male offspring requires more parental investment. Parents in poor condition should be reluctant to invest in the sex that imposes greater demands on resources, due to the risk of reproductive failure in a given episode or impaired reproductive output in the future (i.e., the cost

of reproduction). This would lead to selection of a female-biased sex ratio in the broods of parents in poor condition (Myers 1978). In addition, if variation in parental investment carries over into adulthood and provides fitness benefits for better-nourished males (e.g., during inter-male competition), parents in good condition should produce sons rather than daughters (Trivers and Willard 1973). However, many other factors may significantly influence the brood sex ratio, altering the proportions predicted by theoretical models of adaptive sex allocation. These include environmental factors, age effects, inter-brood competition, timing of breeding, mate quality, etc. (Carranza and Polo 2012; Komdeur 2012; Booksmythe et al. 2017).

The factors shaping adaptive sex ratio allocation require further study, given the conflicting results reported in the literature. This is particularly so as it relates to the application of an experimental approach, as noted by Komdeur and Pen (2002) and Merklings et al. (2012). In this paper, we present the results of an experiment aimed at comparing patterns of brood sex ratio adjustment in the replacement clutches of the Mew Gull (*Larus canus*) and Black-headed Gull (*Chroicocephalus ridibundus*), which are two species that differ in their degree of sexual size dimorphism. We experimentally induced birds to lay replacement clutches while simultaneously providing them with different amounts of supplemental food (see “Methods”) to increase their parental reproductive investment and to differentially improve their condition afterward (see, e.g., Heaney and Monaghan 1995; Nager et al. 1999; Kalmbach et al. 2005; Różycki 2014). In doing so, we mimicked the actual conditions experienced by gulls on our study site at the Vistula River in Poland (Bukaciński et al. 2020). Here, gulls breed on extensive islands and sandbars located within a braided river channel (Chmielewski and Tabor 2017) and suffer heavy losses each year. Frequent increases in the water level, but also mass outbreaks of black flies (*Simuliidae*) and heavy predation by American Minks (*Neovison vison*) and Red Foxes (*Vulpes vulpes*) mean that each year the majority of the breeding population experiences a clutch or brood loss (Bukaciński and Bukacińska 1994, 2000, 2003, 2015a, b). Gulls are long-lived birds and laying replacement clutches repeatedly is costly (Nager et al. 2000b, 2001), which implies possible trade-offs between current and future reproduction (Clutton-Brock 1991; Stearns 1992). This should result in a strong selective pressure to adjust reproductive investment of experimental female gulls to the level of their current individual reproductive capability (e.g., condition) if they decide to reneest. Given consistently high, albeit spatially and temporally unpredictable, clutch losses, gulls of the Vistula river should not refrain from reneesting if they are to produce any offspring in their lifetime. However, they should be selected to adaptively adjust clutch size and egg size in accordance with their current condition if reproductive costs can be

carried over to the next breeding season, as demonstrated by Nager et al. (2001). We were able to demonstrate experimentally that reproductive output in our Mew Gull population is limited by food availability. Pairs that were given supplementary food laid larger clutches, larger eggs, and had enhanced breeding success (Różycki 2014; Wiśniewska 2014; Buczyński unpublished data). Importantly, adaptive sex allocation within the clutch offers some possibility of further adjustment of parental investment, as egg position in the laying sequence is linked to predictable differences in fledging success in gulls (Lundberg and Väisänen 1979; Bukacińska 1999; González-Solis et al. 2005; Kim and Monaghan 2006; Różycki 2014). The chances of survival to adulthood is usually considerably higher for chicks hatching from the first two eggs (A, B) compared to those from a last-laid egg (C). Consequently, the decision of sex allocation across successive eggs in a replacement clutch can be viewed as yet another level of fine-tuning of parental investment. Parents in poor condition should allocate more daughters into C-eggs than parents in good condition, as female chicks will be less susceptible to food shortage during the chick-rearing period.

We should expect that if reproduction in gulls adheres to a mechanism of adaptive sex allocation, the actual sex ratio found in (experimentally induced) replacement clutches should be adjusted in line with the condition of an experimentally manipulated female and the egg position in the laying sequence. Furthermore, we assumed that at least in Mew Gulls (a species with greater sexual size dimorphism), the production of sons is more expensive than daughters. One of the prerequisites was that sexual size dimorphism in this species occurs in the period of post-embryonic chick development, with males being larger and heavier than females close to fledging, although to a lesser extent (at 5–8%) than in adult birds (Table 1, Bukaciński and Bukacińska, in prep.). Unlike other researchers (such as Merklings et al. 2015), we did not measure the actual energy and physiological costs associated with the production of offspring of different sexes. Sexual size dimorphism of chicks may be weakly correlated with the actual differences in the costs of raising sons and daughters (see for example, Torres and Drummond 1999; McDonald et al. 2005). The offspring sex ratio bias towards the ‘cheaper’ sex, which we found in pairs of naturally poorer condition (first clutches vs. replacement clutches, Bukaciński et al. 2020), corresponds well with this basic prediction of the reproductive cost hypothesis (Myers 1978; Cockburn et al. 2002). With this in mind, we expected that (a) parents in poorer condition will over-produce daughters (the presumed cheaper sex) and (b) this relationship will be more evident in a species with greater sexual size dimorphism (Mew Gull, Table 1). We knew from previous studies that food availability is one of the key factors affecting parental condition and reproductive success in our study

Table 1 Sexual size-dimorphism (weight and structural dimensions) in adult Black-headed Gulls (*Chroicocephalus ridibundus*) and Mew Gulls (*Larus canus*)

	Difference between male and female (as a %)			
	Weight (%)	Wing length (%)	Tarsus length (%)	Head and bill length (%)
Black-headed Gull				
Literature data ^a	3–8	3–5	2–5	3–6
Mew Gull				
Literature data ^a	11–15	5–9	5–9	6–9
Middle Vistula River ^{b,c}	12	7	7	8

^aGlutz von Blotzheim and Bauer (1982), Cramp and Simmons (1985), Ilichev and Zubakin (1988)

^bBukaciński and Bukacińska, unpubl. data from the nest trapping in the years 1986–2016

^cBukaciński and Bukacińska (2003)

populations (see above). Considering the generally poor condition of parents during the time that replacement clutches were laid, we expected that supplemental feeding of some (i.e., fed1 and fed2 pairs, see “Methods”) will increase the variance of this trait, and thus increase the room for adaptive manipulation of offspring sex ratio that would be consistent with theoretical predictions of the reproduction cost hypothesis (Myers 1978; Cockburn et al. 2002).

We also wanted to test to what extent the sex ratio pattern found at the stage of egg-laying (primary sex ratio) will change during the first 5 days after hatching (early chick period), when the offspring mortality in the Vistula colonies of these species is at its highest (Bukaciński and Bukacińska 1995; Bukacińska 1999; Buczyński 2000; Pikulska 2017; Korzenecka 2019). We also examined the role of food availability to parents (our experimental treatment), the position of the egg in the laying sequence, and offspring sex, in relation to observed chick mortality patterns.

Methods

Study area and species

The study area included islands in the middle reaches of the Vistula River between Dęblin and the mouth of the Pilica River, Central Poland (km 393–457 of the waterway; 51° 33' 33.88"–51° 51' 45.19" N, 21° 49' 35.86"–21° 16' 58.71" E).

The study was conducted using colonies of Mew Gulls (MG) and Black-headed Gulls (BHG). These species feed on the same items during the breeding season, occupy similar breeding habitats, and nest at the same time (Ostrowska 1995; Bukaciński and Bukacińska 1994, 2003, 2015a, b).

Mew Gull males are 11–15% heavier and 6–9% larger than females, while BHG males are 3–8% heavier and 3–5% larger than females (Table 1). Sexual size dimorphism develops during the first weeks of life and prior to fledging (Bukaciński and Bukacińska in prep.), as is the case in many other size-dimorphic water birds (Becker and Wink 2003; Weimerskirch et al. 2000; Merklings et al. 2012). Every year, a few hundred MG pairs and a few thousand BHG pairs nest at the study location (Bukaciński et al. 2017).

Field data collection

We conducted our study between April and June of 2016. We marked all nests with numbered sticks, checked them every 2 days until clutch completion, and then every 3–5 days until hatching. We marked eggs in clutches as A, B, and C according to their laying order with a non-toxic marker (hereafter referred to as A-egg, B-egg, and C-egg). We ringed the chicks just after hatching and recorded from which egg they hatched as well as the hatching order. We took approximately 40 µl of blood from the tarsal vein of each chick and preserved it in 1 ml of *APS buffer* (Arctander 1988) stored at –20 °C until DNA extraction and PCR analyses. We also collected biological material (liver or heart) from dead chicks in few cases, where they died just prior to planned blood extraction and preserved such material in 1 ml of *Queens Buffer* (Seutin et al. 1991) until molecular analyses. Most adults were individually marked with coloured rings in earlier years. The remaining birds were trapped on their nests and ringed during the study year.

Experimental treatment: a diversification of food availability at breeding sites

On the Vistula River, the breeding season of gulls lasts longer (and the level of investment in egg production is higher) than in other, more stable environments occupied by BHGs and MGs (Glutz von Blotzheim and Bauer 1982; Cramp et al. 1985; Ilichev and Zubakin 1988; Bukaciński and Bukacińska 2003). When planning an experiment, we tried to imitate the natural environmental conditions of the middle Vistula River. Therefore, we used replacement clutches, which are the norm at this study site, rather than the exception (Table 2). Monaghan et al. (1998) found that an increase in production of one egg reduced body weight and protein reserves of Lesser Black-backed Gulls (*Larus fuscus*) by at least 5–6%. Under the Vistula conditions, the weight of MG females incubating replacement clutches was 12–22% lower, depending on the year and individual, in comparison to that of the same birds laying their first clutches (Wiśniewska 2014; Bukaciński and Bukacińska unpublished data). To understand the importance of current food conditions and their effect on biases in offspring

Table 2 Percentage of the Black-headed Gull (*Chroicocephalus ridibundus*) and Mew Gull (*Larus canus*) pairs who lost first clutches and re-nested (from losing pairs) on the middle Vistula River islands in the years 2000–2015

	Number of pairs	Frequency of pairs (as a %)	
		Losing first clutches	Renesting
Black-headed Gull			
Min–max	151–454	43.7–100.0	22.0–77.0
Mean \pm SD	267 \pm 111	57.1 \pm 15.7	41.2 \pm 22.6
Mew Gull			
Min–max	202–444	70.2–100.0	34.0–98.0
Mean \pm SD	334 \pm 94	89.4 \pm 8.8	67.0 \pm 23.2

The range (minimum–maximum) and means with standard deviation (mean \pm SD) are presented

sex ratios in replacement clutches, we induced females from groups of pairs with experimentally differentiated availability of high quality food to re-nest. For the analyses, we used breeding pairs that had begun laying no later than the peak of a given season (i.e., no later than April 25 for BHGs and May 10 for MGs), for which the first and replacement clutches consisted of three eggs.

Due to the fact that frequent increases in water levels, along with significant predation by American Minks and Red Foxes, cause the majority of MG pairs and a large proportion of BHG pairs to quickly lose their clutches (see Table 2), it was necessary to protect three-egg replacement clutches until the time of hatching. For this purpose, we used a method of active gull protection (Bukaciński and Bukacińska 2008; Bukaciński 2015; Bukaciński et al. 2018). Shortly after laying, each egg was taken from the nest to an incubator and a wooden dummy, painted to appear like the original egg, was put in its place. Just before hatching, we returned the clutches from the incubator to the nests from which they were taken. We did not observe any incidents of desertion or less intensive incubation in nests with dummy eggs (Bukaciński 2015; Bukaciński et al. 2018). This was the case both during this study and in earlier and subsequent projects involving active gull protection in Poland.

For both species, we randomly selected three groups consisting of breeding pairs. Two of them we started to feed 12–14 days before laying of the first egg within the breeding territories of particular pairs. After completion of egg-laying, the first clutches from all three groups were removed. That is, the clutches were taken to an incubator and transferred to non-experimental breeding pairs which nested in a similar period but had shortly before hatching produced incomplete clutches (1 or 2 eggs), or whose clutches included some chicks that could not hatch (for reasons of infertile eggs or embryonic death during incubation). This induced experimental females to lay replacement clutches. We ceased feeding of the first group of birds of both species

after the completion of their first clutches (group fed1), the second after completion of their replacement clutches (group fed2), while a third control group was not fed (group unfed). In this way, each of the three groups laying replacement clutches experienced different food conditions. We provided gulls with chopped freshwater fish naturally available from the Vistula River (mainly roach *Rutilus rutilus*; 150–160 g/day/territory). Fish are a valuable, high-protein component of the bird's diet, and the portion size significantly exceeded the daily energy demands of adult birds of both species (see Bolton et al. 1992). Every morning, supplementary food was provided in the territory of each randomly chosen pair, in a permanent place very close to the nest. The control nest sites were visited in the same way as supplemented nests (but no supplementary food was provided). Gulls had no problem finding the place of feeding and effectively defended it against neighbours. Both parents were usually present during feeding. After 2 or 3 days, birds became accustomed to feeding and waited near the territory for extra food. Almost always, it was the female that consumed most of the food portion, while a male defended it against kleptoparasiting neighbours. Even if a large part or the entirety of the food was eaten by a male (if there was no female in the territory), a female received her portion from the male shortly after, either during numerous courtship feedings or as an invitation to copulation (Bukaciński and Bukacińska 2003, 2015a, b).

At the beginning of the breeding season, fragments of islands with nests of fed and unfed pairs were surrounded by an electric fence (see Bukaciński 2015; Bukaciński et al. 2018). Fences hampered (but did not prevent) chicks from moving too far away from the territory, at least during the first 5 days of life when their mobility was low. Most importantly, these fences prevented predation by mammals (i.e., the type of breeding losses that are unrelated to the quality and/or condition of parents or their reproductive tactics). Broods for which there was uncertainty as to how many and which chicks survived to the 5th day after hatching were excluded from the analyses (BHG: 0—unfed, 1—fed1, and 2—fed2; MG: 0, 2, and 2 respectively). Chicks from these nests were last seen on the third or fourth day of life. Following this time, the chicks probably moved beyond the fence. In such cases, we did not know whether their absence during the observed parental feeding attempts was due to movement beyond the fence or the action of avian predators.

Molecular methods

We used either a phenol–chloroform method of DNA extraction (Green and Sambrook 2012) or a GeneMatrix Quick Tissue DNA Purification Kit (EURx) for tissue samples. A salting-out procedure (Miller et al. 1988) or a GeneMatrix Quick Blood DNA Purification Kit (EURx) was used for blood samples. For sex determination, we applied a method

based on amplification of the CHD1 gene intron (*Chromohelicase-DNA-binding gene*) using 2550F and 2718 R primers (Fridolfsson and Ellegren 1999; Ležalova et al. 2005). The 25 µl PCR reaction mixture contained 2.5 µl 10xPCR buffer (EURx), 1.5 µl 25 mM MgCl₂ (EURx), 200 µM each dNTP (EURx), 30 pmol of each primer, and 1 U Taq DNA Polymerase (EURx). Approximately 50–150 ng of genomic DNA was used as a template. Polymerase chain reaction (PCR) was performed in a Biometra TOptical Gradient 96 thermal cycler. We applied the following program: an initial denaturing step at 94 °C for 1 min 30 s, 30 cycles of 48 °C for 45 s, 72 °C for 45 s, 94 °C for 30 s, then 48 °C for 1 min, and final elongation at 72 °C for 5 min (Griffiths et al. 1998; Ležalova et al. 2005). The PCR products were separated for 30 min at 7–10 V/cm using 3% agarose gel stained with ethidium bromide. Males were identified by one band and females by two bands. One known adult male and one known adult female were included in the last line of each gel, as well as a blind sample without DNA.

Statistical analyses

We modelled the variation in sex ratio of chicks of two gull species at two stages of their early lives: at hatching and when a first-hatched chick was 5 days (i.e., following the period of most intense chick mortality occurring shortly after hatching) (e.g., Bukaciński and Bukacińska 1995, 2015a, b; Bukacińska 1999; Buczyński 2000). We used the sex of the chick (0, female; 1, male) as the binary response variable and jointly analysed data from two study species to look for possible between-species differences. We analysed variation in the response variable (effectively, the probability of the chick being male) as a function of three possible predictors: feeding treatment of the parent female prior to laying the replacement clutch, egg position in the laying sequence, and identity of the species. Treatment was coded as a factor with three levels: unfed (control), fed until laying of first clutch (fed1), and fed until laying of replacement clutch (fed2). Egg position in the laying sequence was coded as a factor with three levels: A-egg (first-laid), B-egg (second), and C-egg (third). Species were coded as another factor with two levels (Mew Gull, MG; Black-headed Gull, BHG).

To analyse factors accounting for possible changes in the sex ratio between hatching and the 5th day of life, we analysed survival of chicks until the 5th day (0, died; 1, survived; binary response) as a function of four predictors: treatment, egg position in the laying sequence, species identity, and sex of the chick.

We employed generalized linear mixed models (GLMMs) with a binomial error structure and logit link function to model a relationship between the sex of a focal chick and three candidate predictors in addition to the survival of a chick and four candidate predictors. We applied an

information-theoretic approach (Burnham and Anderson 2002) to find the most parsimonious model among the candidate model set, starting from the most complex (global) model and including all possible simpler models (Grueber et al. 2011). Multiple competing models (with various predictors) were assessed for their fit to the data using Akaike's information criterion corrected for finite samples (AICc). The model selection procedure began from the global model, which included all fixed predictors as main terms and all their two-way interactions (Bolker et al. 2009). We did not use three-way interactions as they are minimally interpretable. This resulted in 18 (chick sex) or 113 (chick survival) models being ranked initially using the AICc criterion. Brood identity (female identity) was included in all models as a random factor. We used R environment (R Core Team 2017) and fit GLMMs with the *lme4* package (Bates et al. 2015). The *MuMIn* package (Bartoń 2017) was used to screen all possible subset models of the global model.

Models differing by less than 6 AICc units from the top-ranked model were initially considered as equally informative (Richards 2008; Richards et al. 2011) and were averaged to obtain parameter estimates and their 95% CIs, while the remaining lower-ranked models were discounted. A natural or conditional averaging method (as opposed to a zero or full method) was applied to obtain weighted parameter estimates across the candidate model set. We then used a "nesting rule" (Harrison et al. 2018) to discount all models that were a more complex version of simpler models having a higher AICc in the candidate model set (Richards 2008, 2015; Richards et al. 2011). For the purpose of transparency, we report these models in tables showing the results of model selection (Tables 3, 5, 7). In addition, we used relative variable importance (RVI) and 95% CIs of model-averaged parameter estimates to decide if a candidate model with a reasonable evidence ratio (usually between 2.5 and 3.5 in our analyses), as compared with the top-ranked model, should be kept in the set of best AIC models (Burnham and Anderson 2002; Anderson 2008). Relative variable importance was used here as a supplementary guide, measuring predictor criticality, rather than true importance (Azen et al. 2001; Galipaud et al. 2017). Candidate models containing "pretending" variables (Anderson 2008; Arnold 2010) were discounted earlier in the analysis using the more stringent Richards (2008) criteria. Applying all of these criteria resulted in the retention of the top model as the sole basis for inference in all three model selection procedures conducted here. We used an *effects* package to estimate fixed factors effects (average model predictions or estimated marginal means) and their 95% confidence intervals (Fox 2003) for the final model.

With respect to experimental group differences, a one-way analysis of variance (ANOVA) was used to check for differences in time-of-breeding and a chi-square test was employed to detect differences in frequencies of broods with

Table 3 Summary of model selection results for GLMMs explaining variation in sex ratio (probability of chick being male), recorded in replacement clutches of two gull species at hatching

No	Model (fixed parameters)	df	LL	AICc	Δ AICc	Weight
1	Treatment + egg + species + treatment:species	9	– 509.143	1036.5	0.00	0.527
(2)	Treatment + egg + species + treatment:species + egg:species	11	– 507.590	1037.5	0.99	0.321
(3)	Treatment + egg + species + treatment:species + treatment:egg	13	– 507.217	1040.9	4.38	0.059
(4)	Treatment + egg + species + treatment:species + treatment:egg + egg:species	15	– 505.647	1041.9	5.39	0.036
5	Treatment + egg	6	– 515.013	1042.1	5.61	0.032

For each model, df is the number of estimated parameters, LL is the model log-likelihood, AICc is the Akaike's information criterion corrected for small samples, Δ AICc is the difference between model's AICc value and the minimum AICc for the whole set of 18 competing models, and weight is Akaike weight for a model. Only models within 6 AICc units from the top model are listed, in ascending order of Δ AICc. For each model, no. = model number, treatment = feeding treatment, species = Mew Gull or Black-headed Gull, egg = egg position within laying sequence. All models had a binomial error structure, with the identity of a brood entered as a random factor. Models that represent more complex versions of simpler models with a lower AICc (and as such should not be considered as the most parsimonious models; see text: "Statistical methods") are indicated with brackets around the model number

variable chick mortality (SPSS 11.0 for Windows; SPSS Inc., Chicago, USA).

Only clutches with a known chick origin (from A-, B-, or C- egg) were included in the analysis ($n = 149$ and $n = 114$ nests of BHGs and MGs, respectively).

Results

Phenology of first and replacement egg-laying

All 149 BHG pairs produced a replacement clutch 12.6 ± 2.5 days (mean \pm SD) after their first clutch was experimentally removed. This time interval was not affected by the feeding treatment (one-way ANOVA, $F_{2,146} = 0.81$, $p = 0.37$). Mean laying dates of first (April 21 ± 5.1 days) and replacement clutches (May 2 ± 5.6 days) did not differ between feeding treatments (one-way ANOVA, $F_{2,146} = 0.66$, $p = 0.42$, and $F_{2,146} = 0.37$, $p = 0.54$, respectively).

Similarly, in the case of MG pairs, we did not find any differences among the experimental groups with respect to the date of laying. All 114 pairs produced a replacement clutch on average 12.3 ± 3.0 days after their first clutch was experimentally removed. This time interval did not differ among feeding treatments (one-way ANOVA, $F_{2,111} = 0.30$, $p = 0.59$). Likewise, the mean laying dates of first (May 7 ± 5.8 days) and replacement clutches (May 23 ± 6.0 days) did not differ among feeding treatments (one-way ANOVA, $F_{2,111} = 0.36$, $p = 0.55$, and $F_{2,111} = 0.53$, $p = 0.47$, respectively).

Due to the fact that we did not record any losses at the incubation stage, there were three eggs in all replacement clutches on the day of hatching, and primary (i.e., during egg laying) and secondary (i.e., shortly before hatching) sex ratios were the same.

Hatching sex ratio

Sex ratio at hatching was affected by our experimental treatment, with additional effects of egg sequence and species identity. The best-supported model of hatching sex ratio included egg sequence, species, treatment, and species \times treatment interaction as fixed predictors (Table 3). Apparently, there was some support for the additional effect of species \times egg sequence, as evidenced by the second-ranked model (evidence ratio 1.64). However, this model was only a more complex version of the top model and model-averaged estimates for this interaction overlapped zero (Table 4), prompting us to discount the possibility that the egg sequence effect differed between species. Likewise, there was no compelling evidence to support inclusion of egg \times treatment interaction as a truly informative parameter (all model-averaged 95% CIs overlapped zero, RVI = 0.10). Therefore, we adopted the AIC-best model (Table 3) as the basis of our inference.

For both gull species, parents that were provided supplemental food had more male chicks at hatching than unfed (control) parents. This was particularly so if they were fed until laying of the replacement clutch. This gradient in hatching sex ratio was much more pronounced in MG than in BHG (Fig. 1), with 69% of male chicks in broods of MG parents fed until laying of the replacement clutch and 27% of male chicks of MG parents not receiving supplemental food (56% vs. 41%, respectively, in BHG).

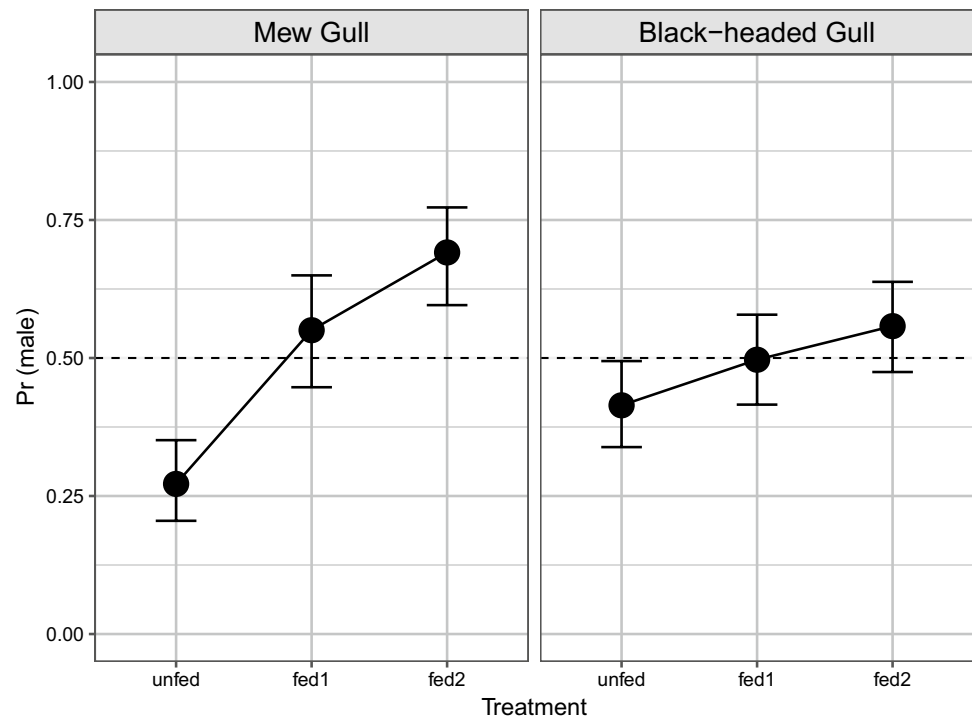
In both gull species, male chicks were also clearly more frequently represented in A-eggs (61%) than in B- or C-eggs (39% and 46%, respectively; Fig. 2). Despite the lack of convincing evidence to support the inclusion of egg \times experiment interaction as a truly informative parameter (see above), we nevertheless present this relationship in Fig. 3. It provides a useful background to explain the mortality rate

Table 4 Model-averaged parameter estimates for the most parsimonious set of candidate GLMMs explaining variation in sex ratio (probability of chick being male) at hatching

Parameter	Estimate	SE	95% CI	
			lower	upper
Intercept	− 0.4701	0.2359	− 0.9330	− 0.0072
Egg (B)	− 0.4701	0.2359	− 1.3279	− 0.2846
Egg (C)	− 0.7038	0.2745	− 1.2424	− 0.1652
Species (BHG)	0.6499	0.2803	0.0996	1.2001
Treatment (fed1)	1.1602	0.3048	0.5621	1.7584
Treatment (fed2)	1.7227	0.3401	1.0553	2.3901
Species (BHG): treatment (fed1)	− 0.8520	0.3694	− 1.5771	− 0.1268
Species (BHG): treatment (fed2)	− 1.2078	0.3716	− 1.9372	− 0.4785
Egg (B): species (BHG)	0.3808	0.3757	− 1.1183	0.3567
Egg (C): species (BHG)	0.2754	0.3742	− 0.4591	1.0099
Egg (B): treatment (fed1)	0.0487	0.4476	− 0.8300	0.9273
Egg (C): treatment (fed1)	0.2985	0.4450	− 0.5751	1.1721
Egg (B): treatment (fed2)	0.4589	0.4448	− 0.4143	1.3321
Egg (C): treatment (fed2)	0.8621	0.4477	− 0.0167	1.7409

Shown are conditional estimates of fixed effects averaged across 5 candidate models with $\Delta\text{AICc} < 6$ (see Table 3). Estimates with 95% CIs not overlapping zero are shown in bold

Fig. 1 Probability of a chick being male at hatching in relation to feeding treatment (unfed—parents receiving no supplemental feed, fed1—parents fed until laying of first clutch, fed2—parents fed until laying of replacement clutch, and species (panels). Modelled means with $\pm 95\%$ confidence intervals from the top-ranked model (Table 3) are shown, based on values extracted from the *effects* package



of chicks of different sexes in the early chick period (see “Results” and “Discussion”).

Sex ratio 5 days post-hatching

Five days after hatching, the sex ratio of surviving chicks was dependent mainly on experimental treatment and egg sequence. Unlike at hatching, we found no important effects

of species \times treatment interaction. As a candidate, the top selected model (containing only additive effects of supplemental feeding and egg sequence) was almost three times more likely than models that included an additional species effect (evidence ratio 2.69) or species and species \times treatment interaction (evidence ratio 3.04; Table 5). With regard to species effect, 95% CIs of the model-averaged estimate did not overlap zero (Table 6); however, the RVI

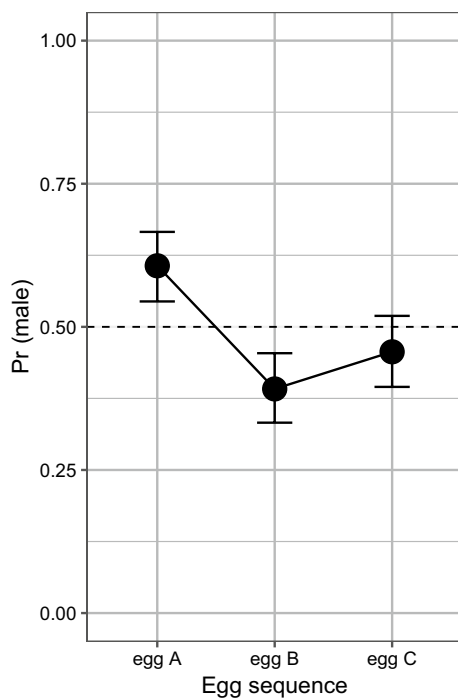


Fig. 2 Probability of a chick being male at hatching in relation to egg position in the laying sequence (egg A: first-laid egg, egg B: second-laid egg, egg C: third-laid egg). Modelled means with $\pm 95\%$ confidence intervals from the top-ranked model (Table 3) are shown, based on the values extracted from the *effects* package

for this variable in the full model set was very low (0.46). Furthermore, models including species effect, alongside with species \times treatment effect, represented cases of nesting issues in model selection (see: *Statistical methods*). This suggested that they should be removed from the candidate set of best models. In addition, the species variable included in the second-best model met the criteria of a "pretending variable" (Anderson 2008; Arnold 2010), with almost the same associated model log-likelihood as the top model (-369.535 vs. -369.571) and with a difference in AICc close to two (1.98). We, therefore, conclude that treatment and egg sequence are the single best predictors of sex ratio among 5-day-old chicks of both gull species.

As at the time of hatching, on the fifth day of life the brood sex-ratio was clearly male-biased in parents receiving supplemental feeding in both gull species. However, differences between treatments were less extreme than at hatching. Broods of gull parents receiving supplemental food until laying of a replacement clutch contained 55% male chicks, while among unfed parents this proportion averaged 40% (Fig. 4).

In both gull species, chicks who survived until the 5th day of life and hatched from first-laid eggs (A-eggs) were predominantly male (62%), whereas chicks from B- and C-eggs were mostly female (40% and 44% male, respectively; Fig. 5). These results were independent of feeding treatment.

Fig. 3 Probability of chick being male at hatching in relation to egg position in the laying sequence (egg A: first-laid egg, egg B: second-laid, egg C: third-laid egg) and to feeding treatment (unfed—parents receiving no supplemental feed, fed1—parents fed until laying of first clutch, fed2—parents fed until laying of replacement clutch). Modelled means with $\pm 95\%$ confidence intervals from the third-ranked model (Table 3) are shown, based on the values extracted from the *effects* package

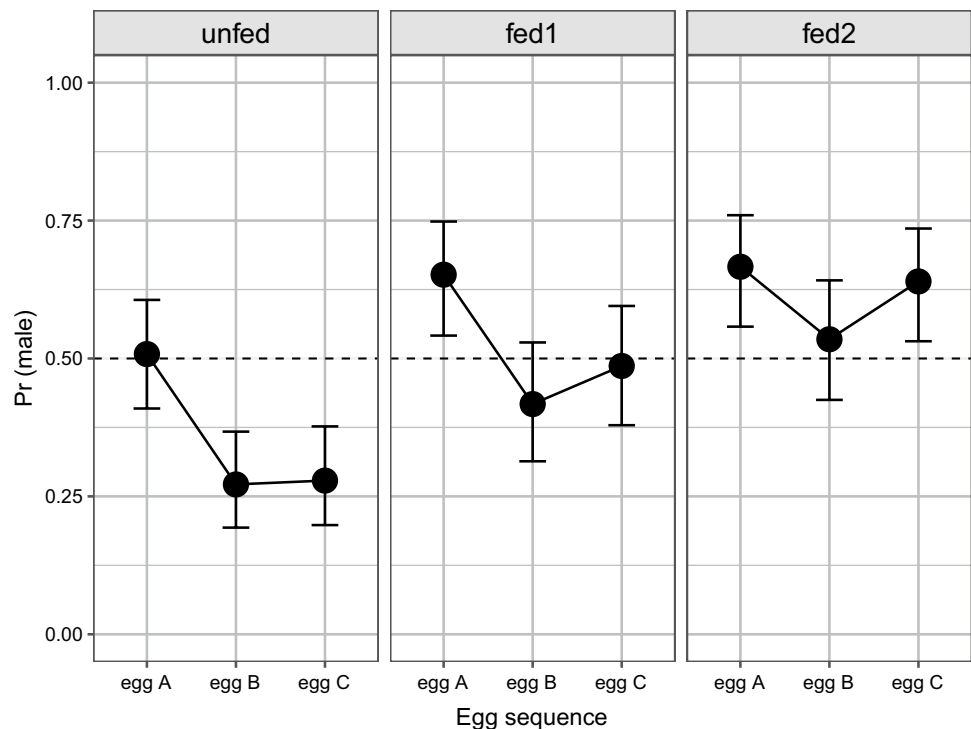


Table 5 Summary of model selection results for GLMMs explaining variation in sex ratio (probability of chick being male), recorded in replacement clutches of two gull species at 5 days post hatching

No	Model (fixed parameters)	df	LL	AICc	Δ AICc	Weight
1	Treatment + egg	6	− 369.571	751.3	0.00	0.462
(2)	Treatment + egg + species	7	− 369.535	753.3	1.98	0.172
(3)	Treatment + egg + species + egg:species	9	− 367.594	753.5	2.22	0.152
4	Egg	4	− 373.588	755.2	3.95	0.064
(5)	Treatment + egg + species + treatment:species	9	− 368.791	755.9	4.62	0.046
(6)	Treatment + egg + species + treatment:species + egg:species	11	− 366.808	756.1	4.81	0.042
(7)	Egg + species	5	− 373.579	757.3	5.97	0.023

For each model, df is the number of estimated parameters, LL is the model log-likelihood, AICc is the Akaike's information criterion corrected for small samples, Δ AICc is the difference between model's AICc value and the minimum AICc for the whole set of 18 competing models, and weight is Akaike weight for a model. Only models within 6 AICc units from the top-model are listed (in ascending order of Δ AICc). For each model, no. = model number, treatment = feeding treatment, species = Mew Gull or Black-headed Gull, egg = egg position within laying sequence. All models had a binomial error structure, with identity of brood entered as random factor. Models that represent more complex versions of simpler models with a lower AICc (and as such should not be considered as the most parsimonious models; see text: “Statistical methods”) are indicated with brackets around the model number

Table 6 Model-averaged parameter estimates for the most parsimonious set of candidate GLMMs explaining variation in sex ratio (probability of chick being male) at 5 days post-hatching

Parameters	Estimate	SE	95% CI	
			Lower	Upper
Intercept	− 0.4761	0.2344	− 0.9361	− 0.0162
Egg (B)	− 0.7917	0.2521	− 1.2864	− 0.2970
Egg (C)	− 0.6683	0.2413	− 1.1418	− 0.1948
Species (BHG)	0.6332	0.2937	0.0567	1.2098
Treatment (fed1)	1.1575	0.3004	0.5679	1.7471
Treatment (fed2)	1.7481	0.3230	1.1144	2.3818
Species (BHG): treatment (fed1)	− 0.8501	0.3691	− 1.5746	− 0.1256
Species (BHG): treatment (fed2)	− 1.2072	0.3715	− 1.9364	− 0.4779
Egg (B): species (BHG)	− 0.3806	0.3759	− 1.1185	0.3574
Egg (C): species (BHG)	0.2752	0.3739	− 0.4589	1.0092

Shown are conditional estimates of fixed effects averaged across 7 candidate models with Δ AICc < 6 (see Table 5). Estimates with 95% CIs not overlapping zero are shown in bold

Survival during the first 5 days post-hatching

The top-ranked model revealed that chick survival during the first 5 days of life was primarily dependent on sex, species, egg sequence, and treatment (with an added effect of sex \times treatment interaction) (Table 7). The model ranked as second-best differed in that it lacked a species variable and inclusion of this predictor was not supported by model-averaged effects (95% CIs included zero; Table 8). However, this predictor showed an acceptable RVI (0.77) and no nested model lacking this predictor had a higher AICc. We, therefore, treated species as an informative variable, unlike a number of interactions appearing in lower-ranked models that were discounted because of the presence of simpler, nested models with a lower AICc.

Chicks hatched from a last-laid (C) egg in a clutch had a much lower probability of survival (39%) than chicks from

the first two eggs (A-egg 97%, B-egg 91%), irrespective of sex, treatment, or species (Fig. 6). Supplementary feeding was associated with improved chick survival for both gull species, though this effect was dependent on chick gender (Fig. 7). In control broods, in which parents did not receive any food, male chicks survived better than female chicks (77% vs. 61%), but the opposite was true for broods, where parents received food. In broods tended by parents fed until laying of the first clutch, male chicks had lower survival than female chicks (83% vs. 91%). Similarly, broods with parents fed until laying of a replacement clutch showed the highest rates of survival compared to any other treatment; however, males survived less frequently than females (87% vs. 98%). There was an overall tendency for higher survival of BHG chicks compared to MG chicks (88% vs. 81%).

In all experimental groups, the frequency of broods with chicks lost in the early chick period was uneven

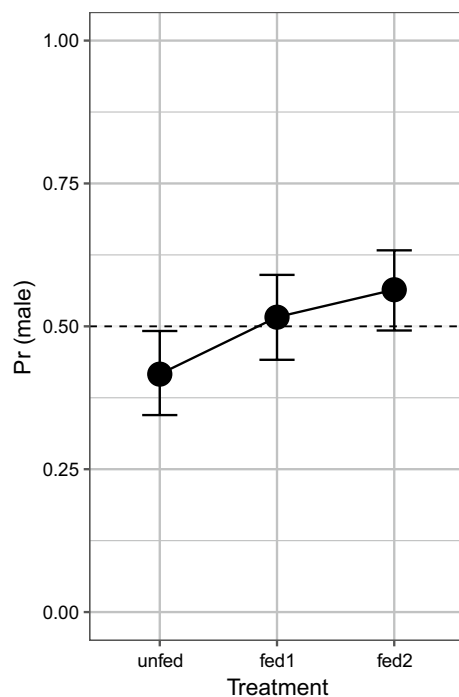


Fig. 4 Probability of chick being male at the 5th day post-hatching in relation to feeding treatment (unfed—parents receiving no supplemental feeding, fed1—parents fed until laying of first clutch, fed2—parents fed until laying of replacement clutch). Modelled means with $\pm 95\%$ confidence intervals from the top-ranked model (Table 5) are shown, based on the values extracted from the *effects* package

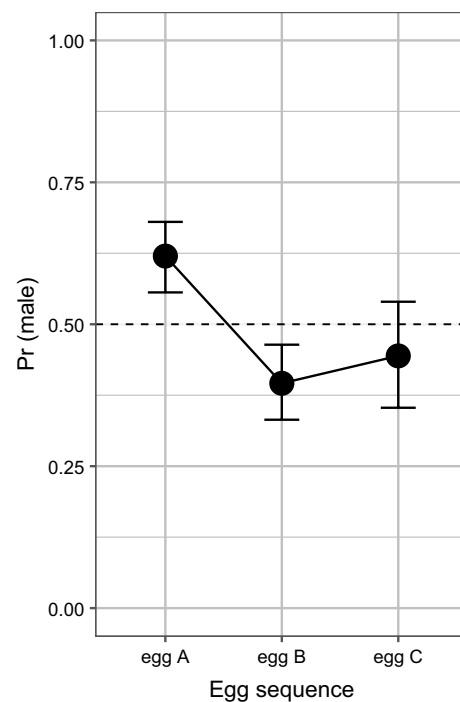


Fig. 5 Probability of chick being male at the 5th day post-hatching in relation to egg position in the laying sequence (egg A: first-laid egg, egg B: second-laid egg, egg C: third-laid egg). Modelled means with $\pm 95\%$ confidence intervals from the top-ranked model (Table 3) are shown, based on the values extracted from the *effects* package

($\chi^2_3 = 11.84\text{--}41.68$, $p < 0.001$, depending on the treatment). Broods with no losses during the first 5 days post-hatching were most frequently represented among the experimental group whose parents were fed until laying of the replacement clutch, while the opposite was true for unfed parents (50.6% and 22.0%, respectively; $\chi^2_3 = 12.22$, $p = 0.002$; Fig. 8a). When parents lost their offspring, it was most common to lose one chick (as was the case in 43.3–52.5% of all broods, depending on the treatment), whereas total losses were recorded relatively more often in broods of control pairs (unfed) as compared to broods of fed parents (13.0%, 3.8%, and 6.0%, for the unfed, fed1 and fed2 groups, respectively; $\chi^2_6 = 52.47$, $p \ll 0.001$; Fig. 8a).

In broods of control pairs in which no chicks survived, male chicks prevailed in only 23.1% of them, while in the broods of parents fed until laying of a replacement clutch, male chicks prevailed in all of them, including 80% of cases in which all three chicks were male ($\chi^2_2 = 8.85$, $p = 0.01$; Fig. 8b).

Discussion

Replacement clutches: an indicator of good parental quality, reproductive tactics, or environmental constraint?

Egg production is one of the most expensive components of parental effort in birds and affects the body condition of mothers (e.g., Bolton et al. 1992; Bauch et al. 2010). In the Lesser Black-backed Gull, the laying of one extra egg above the standard three results in a 5–6% decrease in body weight and protein reserves (Monaghan et al. 1998). Renesting for gulls is, therefore, a difficult and risky action, especially because their current reproductive investment can affect future reproductive output, survival, and fitness (Monaghan et al. 1998; Nager et al. 2001; Kalmbach et al. 2004). Renesting is considered an indicator of the good quality and/or condition of parents (Roonem and Robertson 1997; Hipfner et al. 1999; Wendeln et al. 2000; Becker and Zang 2011). This behaviour can also be associated with more extensive parental experience and/or older age (Wooller 1980; Wendeln et al. 2000; Arnold et al. 2010). In the BHG and MG colonies of the Vistula River (as well as in other breeding grounds), the oldest/most experienced and/or good-quality birds begin breeding first (Onno 1967; Kharitonov 1975;

Table 7 Summary of model selection results for GLMMs explaining probability of chick surviving until 5th day post-hatching, recorded in replacement clutches of two gull species

No	Model (fixed parameters)	df	LL	AICc	Δ AICc	Weight
1	Treatment + egg + species + sex + treatment:sex	10	– 348.114	716.5	0.00	0.355
2	Treatment + egg + sex + treatment:sex	9	– 349.757	717.7	1.23	0.191
(3)	Treatment + egg + species + sex + treatment:sex + species:sex	11	– 347.983	718.3	1.79	0.145
(4)	Treatment + egg + species + sex + treatment:sex + egg:species	12	– 347.799	720.0	3.49	0.062
(5)	Treatment + egg + species + sex + treatment:sex + egg:sex	12	– 347.984	720.4	3.86	0.052
(6)	Treatment + egg + species + sex + treatment:sex + treatment:species	12	– 348.351	721.1	4.59	0.036
(7)	Treatment + egg + sex + treatment:sex + egg:sex	11	– 349.619	721.6	5.07	0.028
(8)	Treatment + egg + species + sex + treatment:sex + species:sex + egg:species	13	– 347.697	721.9	5.35	0.024
(9)	Treatment + egg + species + sex + treatment:sex + species:sex + egg:sex	13	– 347.920	722.3	5.80	0.020

For each model, df is the number of estimated parameters, LL is the model log-likelihood, AICc is the Akaike's information criterion corrected for small samples, Δ AICc is the difference between model's AICc value and the minimum AICc for the whole set of 113 competing models, and weight is Akaike weight for a model. Only models within 6 AICc units from the top model are listed, in ascending order of Δ AICc. For each model, no. = model number, treatment = feeding treatment, species = Mew Gull or Black-headed Gull, egg = egg position within laying sequence, sex = sex of the chick (0, female; 1, male). All models had the binomial error structure, with identity of brood entered as random factor. Models that represent more complex versions of simpler models with a lower AICc (and as such should not be considered as the most parsimonious models; see text: "Statistical methods") are indicated with brackets around the model number

Table 8 Model-averaged parameter estimates for the most parsimonious set of candidate GLMMs explaining probability of chick surviving until 5th day post-hatching

Parameter	Estimate	SE	95% CI	
			Lower	Upper
Intercept	1.8436	0.4264	1.0067	2.6804
Egg (B)	– 1.0788	0.3574	– 1.7804	– 0.3773
Egg (C)	– 3.8652	0.4689	– 4.7857	– 2.9447
Sex (male)	0.7835	0.4469	– 0.0938	1.6607
Species (BHG)	0.5105	0.3823	– 0.2400	1.2609
Treatment (fed1)	1.7917	0.4747	0.8599	2.7235
Treatment (fed2)	3.2652	0.6172	2.0536	4.4768
Sex (male): treatment (fed1)	– 1.4113	0.6049	– 2.5986	– 0.2239
Sex (male): treatment (fed2)	– 2.5917	0.6932	– 3.9524	– 1.2310
Sex (male): species (BHG)	0.2543	0.4963	– 0.7200	1.2286
Egg (B): species (BHG)	0.2700	0.6288	– 0.9643	1.5043
Egg (C): species (BHG)	– 0.1530	0.6118	– 1.3540	1.0479
Egg (B): sex (male)	– 0.2685	0.6791	– 1.6016	1.0646
Egg (C): sex (male)	– 0.3413	0.6542	– 1.6256	0.9429
Species (BHG): treatment (fed2)	– 0.0205	0.6803	– 1.3559	1.3149
Species (BHG): treatment (fed2)	0.1218	0.6951	– 1.2427	1.4863

Shown are conditional estimates of fixed effects averaged across 9 candidate models with Δ AICc < 6 (see Table 7). Estimates with 95% CIs not overlapping zero are shown in bold

Fjeldsa 1978; Rattiste and Lillileht 1987; Różycki 2014). Considering that all experimental pairs began laying their first clutches no later than during the peak of the laying season, it is quite likely that most of them belonged to the fraction of the oldest and most experienced birds.

However, it is problematic to assume that under the Vistula River conditions, the individual characteristics of a bird have a key impact on the decision to lay a replacement clutch (and determine the frequency of such behaviour in the

population). Which and how many gulls will reneest is a function of timing and the magnitude of spring floods on the Vistula River and the temporal/spatial variation in mammalian predation of first clutches. In each of the last 16 breeding seasons (2000–2015), on average nearly 90% of MG pairs and ca. 60% of BHG pairs lost their first clutches. Of these, up to 77–98% laid a replacement clutch (Table 2). It cannot be assumed that such a large fraction was represented only by the highest quality, most experienced, and oldest birds in

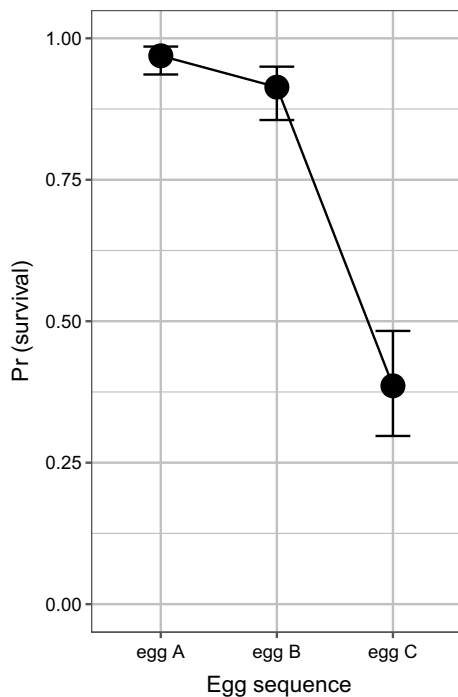
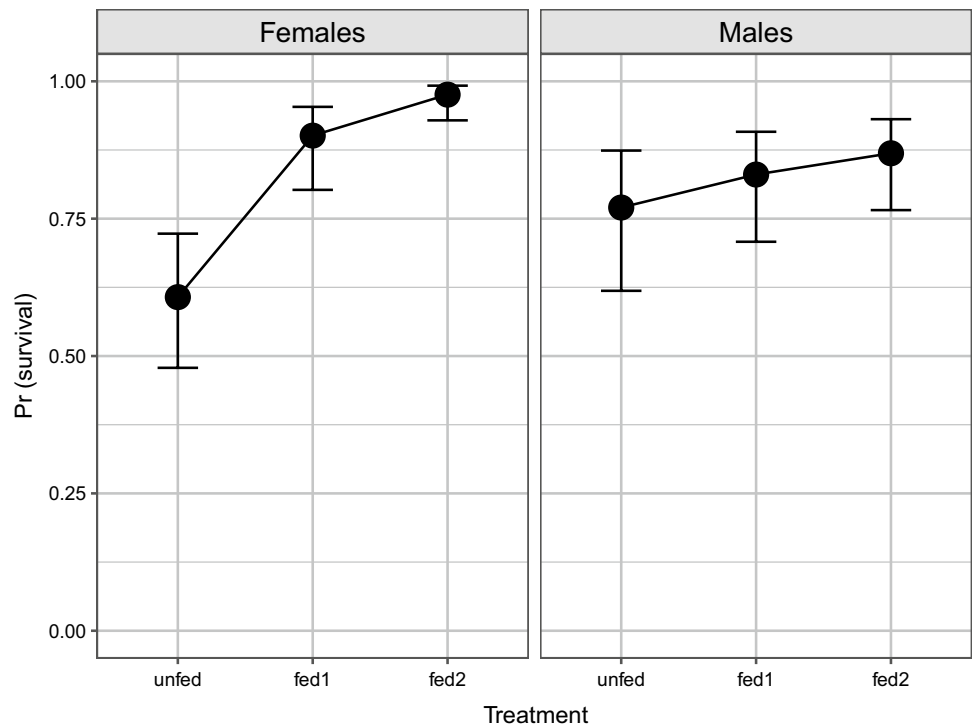


Fig. 6 Probability of chick surviving until the 5th day post-hatching in relation to egg position in the laying sequence (egg A: first-laid egg, egg B: second-laid egg, egg C: third-laid egg). Modelled means with $\pm 95\%$ confidence intervals from the top-ranked model (Table 7) are shown, based on the values extracted from the *effects* package

the populations of both species. A large proportion of breeding losses was the result of flooding, at which time birds lost their clutches and then engaged in synchronous re-laying of eggs. There is a possibility that for some pairs (in the case of either young and/or inexperienced birds), re-nesting might be a kind of "contagious behaviour" induced by courtship behaviour of neighbours (see Bukacińska 1999). A similar rapid and widespread re-laying in response to flooding of first clutches has been reported for other gull and tern species (Storey 1987; Brown and Morris 1996).

Interspecies differences in the frequency of losses resulted mainly from the fact that BHGs begin their breeding season earlier and inhabit the highest islands and/or parts of islands flooded less frequently, as compared to the lower breeding sites of MGs (Bukaciński and Bukacińska 1994, 2015a, b). As was especially the case for MG, a species with high natal philopatry and very strong nesting site tenacity (Rattiste and Lilleleht 1986; Bukaciński and Bukacińska 2003, 2015a), the decision to lay a replacement clutch seems more obligatory than a choice. Failure to re-nest (regardless of individual features) could result in birds having only one or two further chances of successfully breeding during their lifetime. In extreme situations, there may very well be no further chances of breeding. We believe that in the Vistula River conditions, re-nesting individuals of MG (and perhaps also BHG) would achieve higher lifetime reproductive success (a proxy for fitness) compared to birds that refrain from re-nesting, similar to what has been shown for the Common Tern (*Sterna hirundo*) by Becker and Zang (2011).

Fig. 7 Probability of chick surviving until the 5th day post-hatching in relation to feeding treatment (unfed—parents receiving no supplemental feeding, fed1—parents fed until laying of first clutch, fed2—parents fed until laying of replacement clutch) and the sex of the chick. Modelled means with $\pm 95\%$ confidence intervals from the top-ranked model (Table 7) are shown, based on the values extracted from the *effects* package



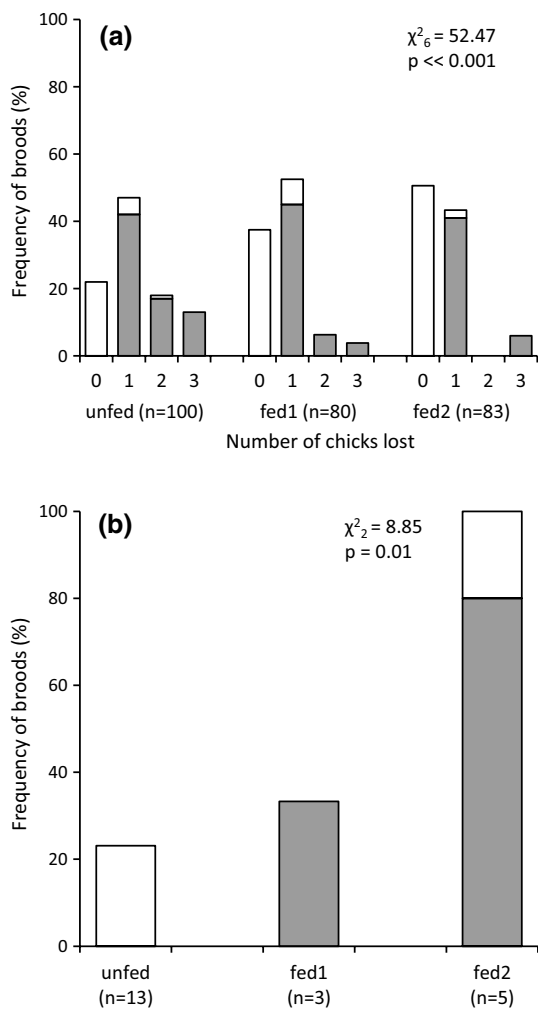


Fig. 8 Combined brood frequency (expressed as a %) of Mew Gulls (MG) and Black-headed Gulls (BHG) having **a** 0, 1, 2, and 3 chicks lost between hatching and the fifth day of life (with the shaded area representing the percentage of broods in which one of the lost chicks was a C-egg) and **b** total losses (in which male chicks predominated). The shaded area represents the percentage of broods in which all chicks were males. Recall that all broods initially had three chicks. n number of nests, χ^2 chi-square test statistic, p predicted probability, * $p < 0.05$, other explanations as in Fig. 1

On the Vistula River, BHGs commence egg laying around mid-April and ending in the last days of May, with the peak of egg-laying occurring in the last days of April (Bukaciński and Bukacińska 1994, 2015b; Bukacińska and Bukaciński unpublished data). Mew Gulls begin egg laying in the last days of April and complete the first laying in late May or early June, with the peak of egg-laying occurring between May 1 and 10 (Bukaciński and Bukacińska 1994, 2003, 2015a). Our long-term data from this population reveal that if a rise in water level destroys clutches in late April or early May (i.e., during the period when we removed the first clutches as part of our experiment), most of the BHG and almost all MG pairs usually

begin to lay replacement clutches. It was, therefore, not particularly surprising that all studied pairs attempted to breed again, especially given the fact that we removed the first clutches immediately after their completion, at a time when parental investment related to incubation had just begun (Bukacińska 1999; Bukaciński and Bukacińska 2003). However, we did not expect that all pairs would again lay three-egg clutches, regardless of whether and for how long they were given supplementary food. This result clearly indicates that parents prefer to lay a new, complete 3-egg replacement clutch and adjust offspring sex ratio, than to modify parental expenses by laying fewer eggs. This is particularly interesting, because sex ratio manipulation is often considered to be only a minor adjustment of parental expenditure (and represents a smaller adjustment compared to egg-laying; see Carranza 2004; Carranza and Polo 2012). In light of this, a smaller replacement clutch would be expected. The occurrence of a large number of 3-egg replacement clutches was likely due to the fact that such losses occurred early in the season when the most experienced and best quality birds began to breed. These birds were also in the best condition, as shown by other studies of the Vistula colonies (Różycki 2014). It is also important that the loss of a clutch occurred at a very early stage of reproduction (shortly after completion of the first clutch) when parents are more willing to lay 3-egg replacement clutches (Bukacińska 1999). Earlier data from our study site show that if a natural flood took the clutches of most BHG and MG pairs at a similar time and a similar breeding stage, then 3-egg clutches were still predominant among replacements (although such cases accounted for only 45–70% of clutches) (Buczyński 2000; Bukacińska 1999; Różycki 2014). The contribution of 2-egg replacement clutches ranged from 25 to 45%, while those comprising one egg were never greater than a few percent (Buczyński 2000; Bukacińska 1999; Różycki 2014).

We know from previous studies that when the loss of first clutches of BHG and MG occurred later in the season and at a later breeding stage, a smaller number of pairs will lay a replacement clutch. Furthermore, the proportion of 2- and 1-egg clutches will be greater and will occur at the expense of replacement clutches containing 3 eggs (Bukacińska 1999; Różycki 2014; Bukaciński and Bukacińska unpublished data). These data show that gulls will more often reduce the size of a replacement clutch rather than forgo reneating. Taken together, these data indicate that the decision to attempt the laying of a replacement clutch might be a default behaviour rather than a strategic choice. In contrast, the number of eggs laid in such a clutch and the resulting sex-ratio of chicks appears to be more affected by the condition of parents and their reproductive tactics.

Hatching sex ratio in broods of BHGs and MGs: the effect of food availability

Regardless of whether reneating is a choice made by higher quality birds and/or birds in better condition, a feature of the oldest and/or most experienced individuals, or is a default decision for the majority of gulls living in a highly unstable environment, expenditures incurred at the time of a first clutch (as they are related to a decrease in body mass and protein reserves in females; Monaghan et al. 1998; Wiśniewska 2014; Bukaciński and Bukacińska unpublished data) should compel parents to optimize their efforts later in the breeding season. Such considerations should also apply to primary sex-ratio biases.

The condition of parents during the period of reneating is generally poorer and the availability of food in the breeding grounds affects the level of brood sex ratio bias in both gull species. As shown by Nager et al. (1999) for Lesser Black-backed Gulls, Alonso-Alvarez and Velando (2003) and Pérez et al. (2006) for Yellow-legged Gulls (*Larus cachinnans/Larus michahellis*), and Merklings et al. (2012) for Black-legged Kittiwakes, we found that unfed parents overproduced daughters (i.e., the cheaper sex). In contrast, fed parents, especially those fed the longest, overproduced sons (Fig. 1). The sex ratio bias in the replacement clutches of BHGs and MGs found at hatching was in line with the theoretical predictions of the reproductive cost hypothesis (Myers 1978; Cockburn et al. 2002). Moreover, this relationship was much stronger in broods of MG, a species for which there are potentially larger differences in the costs of raising daughters and sons (as judged by body size dimorphism, though this assumption was not validated in this study). This is in contrast to broods of BHG, which are characterized by significantly less sexual size dimorphism. The much lower frequency of sons produced by unfed MG pairs might suggest that in this species (and to a greater extent than in BHGs) the larger sex may require more time and/or nutrition/energy expenditures during the growth period, especially when parents are in poor condition (Myers 1978; Cockburn et al. 2002). This would be in agreement with the reproductive cost hypothesis.

Unlike for broods of experimentally fed BHG and Black-legged Kittiwakes pairs, which had a balanced sex ratio at hatching (Fig. 1; Merklings et al. 2012), the broods of MG parents fed until laying of a replacement clutch (fed2) were strongly male-biased (69% males, Fig. 1). This pattern is not inconsistent with the interpretation of the reproductive cost hypothesis, if we assume that parents in better condition (fed) are more likely to take the risk of producing offspring of the more expensive sex (i.e., the sex that is more physiologically and/or energetically demanding to produce). However, it is also consistent with the basic premise of Trivers–Willard hypothesis, given strong inter-male

competition over access to best nesting sites and best mates observed in gulls in general (e.g., Southern 1981; Butler and Janes-Butler 1983; Bukacińska and Bukaciński 1993; Bukaciński and Bukacińska 1996, 2003; Bukaciński 1998). Larger size dimorphism in MG than in BHG is suggestive of more intense intra-sexual competition in the former species, resulting in greater benefits of producing good quality, competitive sons by MG in presumed best condition (fed2 group). Yet, given the data available, we cannot really offer a compelling explanation for overproduction of males by MG parents in best condition.

It is worth noting that in both Vistula gull species, sons hatched significantly more often from A-eggs (first-laid) compared to B- and C-eggs (Fig. 2). Moreover, only in A-eggs was the proportion of sons at hatching never less than 0.5 (Fig. 3). In fed pairs, the proportion of sons from each of the three eggs was higher than for unfed pairs, though the difference was greater for chicks hatched from last-laid eggs (C-eggs) compared to those hatched from either A- and B-eggs (Fig. 3). It was the most prevalent offspring sex from the first and last eggs in a brood at hatching that had the greatest impact in shaping sex bias among siblings during the chick period. Chicks from C-eggs in the Vistula River populations of MG and BHG are on average the smallest. They often hatch slightly later than offspring from A- and B-eggs and thus are more prone to dying prematurely compared to their siblings. This is especially the case during food shortages and/or when the condition of their parents is poor (Dejtrowski 1993; Buczyński 2000; Różycki 2014). This is often the reason why chicks leave their own brood-mates to join the broods of neighbours (Bukaciński et al. 2000; Bukaciński and Bukacińska 2015a, b). In contrast, the offspring from A-eggs have the highest status (usually hatching first) and generally win the competition for food with their siblings (Bukacińska 1999; Różycki 2014). In the species that produce several offspring per reproductive attempt (as with MG and BHG), parental resources must be divided among siblings. In such cases (and as Carranza (2004) has noted), the resources obtained by a single chick will depend not only on the total parental resources but also on the number and sex of competing siblings and the interactions between them (Kalmbach et al. 2005; Uller 2006). From this perspective, the optimal sex order of siblings should be arranged in a hierarchical fashion based on their expected share in parental resources, which may lead to a lack of correlation between parental resources and the brood sex ratio (Carranza 2004).

Sex ratio 5 days post-hatching: the effect of sex-biased mortality

As at hatching, on the fifth day of chick life the brood sex ratio was biased towards males among parents receiving

supplemental food, though with two significant differences: (a) the extent of bias in MG broods was clearly smaller than at hatching, which as a consequence meant that (b) we no longer observed significant differences in this parameter between the two gull species (Fig. 4). This may indicate that sexual size dimorphism was not very important in shaping the brood sex ratio bias in MG and BHG.

Contrary to our prediction that sons will be more susceptible to poor food conditions, daughters instead experienced greater mortality. The lack of mortality differences between species in the early-chick period indicates that this relationship was stronger in MG than BHG broods. To explain this, we must take into account the following: (1) all broods of control pairs with total losses (13.0% of all broods) were female-biased, including almost 80% with only daughters (Fig. 8); (2) parents of all experimental groups (and both species) most often lost only one chick (60.3–87.0% of broods with losses, depending on the experimental group), including 85.7–94.4% for which there was a chick hatched from a C-egg (Fig. 8); and (3) that among the offspring from C-eggs of unfed parents, daughters accounted for nearly 75% of chicks at hatching. There is no doubt that the key mechanism shaping this situation was competition among siblings and the condition of parents (i.e., if we accept the assumption that the poorer the condition of parents, the more daughters in the brood). More than half of the sons of control pairs hatched from A-eggs and these chicks had a probability of survival that was nearly 100%. With the observation that males were produced from 30% of B-eggs [and with a probability of survival over 90% (Fig. 6)], we can see that the rank of the egg from which the offspring of a given sex hatched had a decisive impact on the overall brood sex ratio bias during the early-chick stage.

The same factors that determined higher daughter mortality in unfed (control) parents than for sons resulted in higher (as compared to daughters) son mortality in broods of fed parents, especially those fed for longer periods (Fig. 7). Among the offspring of C-eggs of this group of parents, sons comprised nearly 70% of the chicks at hatching (Fig. 3). In the control group, female-biased broods with total losses constituted the majority. In all such broods of fed2 pairs, there were at least two sons (and in 80% of these all offspring were male) (Fig. 8). The laying order of eggs of different sexes and differential mortality of sons and daughters in the post-embryonic period shapes brood sex-ratio bias. This has been demonstrated for Lesser Black-backed Gulls, Herring Gulls *Larus argentatus*, and Common Terns (Nager et al. 1999, 2000a, b; Cook and Monaghan 2004; González-Solís et al. 2005; Kim and Monaghan 2006).

The sex ratio bias in the broods of MG and BHG observed in this study is consistent with the theoretical predictions of the reproductive costs hypothesis (Myers 1978; Cockburn et al. 2002). Even if at the fledging stage the brood sex bias

in these gull species was smaller than that of the early-chick stage, it would not necessarily mean that there is no adjustment of brood sex bias by parents. The Carranza and Polo (2012) model shows that the relationship between parental resources and brood sex ratio can be more complex than is commonly thought. Reviews that have examined the issue of brood sex ratio indicate that the condition of parents more often affects the sex of offspring in a specific position in the brood hierarchy or egg-laying sequence, rather than the sex ratio of the entire brood (Pike and Petrie 2003; Alonso-Alvarez 2006). Carranza and Polo (2012) have demonstrated that when the brood size varies widely (as is the case for MG and BHG), we should not expect a general relationship between parental expenditure and the brood sex ratio. Even in species with sexual size dimorphism, we should not predict a positive, monotonic relationship between parental expenditure and brood sex ratio; a negative relationship may be more likely instead (Carranza and Polo 2012).

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Affiliations

Dariusz Bukaciński¹  · Monika Bukacińska¹ · Przemysław Chylarecki²

¹ Institute of Biological Sciences, Cardinal Stefan Wyszyński University of Warsaw, Wóycickiego 1/3, 01-938 Warsaw, Poland

² Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warsaw, Poland