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Extrapair copulations are frequent but unsuccessful in a highly colonial seabird, the little auk, *Alle alle*

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Sperm competition theory predicts that colonially breeding birds, such as many seabirds, should be exposed to high risks of sperm competition because there are many potential mating partners and severe socioecological constraints on mate-guarding behaviour. However, parentage studies have usually revealed a low frequency of extrapair paternity in colonial seabirds. Detailed studies of copulation behaviour could provide valuable insights into the causality of genetic monogamy in these species. We investigated the timing, frequency and success of extrapair and within-pair copulation attempts in the little auk, a socially monogamous and highly colonial seabird that raises only a single chick per year. We found that the majority of monitored individuals (above 60% in both sexes) engaged in extrapair copulation activities. Extrapair copulation attempts made up usually more than 10% of all copulation attempts of a particular individual but were generally unsuccessful because of female rejection behaviour. Only 2% (8/330) of all copulations with cloacal contact were extrapair copulations. Molecular parentage analysis of 64 chicks revealed only two cases of extrapair paternity, which is comparable to the proportion of successful copulations that were extrapair. We conclude that genetic monogamy seems to be maintained at a proximate level through female resistance to male extrapair copulation attempts and frequent within-pair copulations. Nevertheless, not all extrapair copulations were rejected by females, which suggests that engaging in one or a few extrapair copulations could be adaptive to females, for example as an insurance against mate infertility.
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Comparative analyses have shown that the occurrence of extrapair paternity in birds is closely associated with major life history strategies and patterns of parental care (Bennett & Owens 2002). Typically, species with long adult life span and biparental care are genetically monogamous, whereas extrapair paternity is common in species with 'faster' life histories and less need for male parental care (Mauck et al. 1999; Arnold & Owens 2002). As these basic life history traits diverged early in the phylogenetic history of avian lineages, much of the interspecific variation in extrapair paternity in birds can be explained at the taxonomic levels of orders and families (Arnold & Owens 2002; Bennett & Owens 2002). Variation in extrapair paternity among closely related species is more likely to be explained by variation in certain ecological factors, such as breeding density and synchrony (Westneat & Sherman 1997; Petrie & Kempenaers 1998; Arnold & Owens 2002; Griffith et al. 2002). In particular, colonial breeding should promote extrapair copulation because there is a high encounter rate with potential mating partners, and there are usually strong ecological constraints on mate guarding set by the competition for nest sites (Birkhead et al. 1987; Møller & Birkhead 1993a).

Colonial seabirds are particularly interesting in this respect because the group consists of several taxonomically diverse lineages, all with typically 'slow' life histories and hence an evolutionary predisposition for genetic monogamy. On the other hand, colonial breeding should facilitate extrapair mating behaviour and the risk of sperm competition would thus be expected to be higher among colonial breeders than among solitary breeders within these lineages. The empirical evidence of extrapair paternity in colonial seabirds suggests it occurs at a generally low frequency (Bennett & Owens 2002; Griffith et al. 2002), although with some notable exceptions (Graves et al. 1992; Burg & Croxall 2006; Jouventin et al. 2007). On the other hand, many behavioural studies have found a high frequency of extrapair copulations in colonial seabirds (Hatchwell 1988; Hunter et al. 1992; Wagner 1992a; Møller & Birkhead 1993b). A resolution of this apparent paradox requires detailed behavioural studies that might reveal the functional significance of extrapair copulations and potential conflicts of reproductive interests between the sexes. There are basically two alternative explanations for the low frequencies of extrapair

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paternity in colonial seabirds. (1) Extrapair copulations involve sperm transfer and lead to sperm competition, but have low fertilization success because of frequent within-pair copulations (Birkhead et al. 1987) and/or females selectively eject sperm from extrapair males. Sperm ejection has been documented in species where females have multiple partners (Davies 1983; Pizzari & Birkhead 2000) as well as in more sexually monogamous and colonial seabirds (Wagner et al. 2004). (2) Extrapair copulations do not generally involve the transfer of sperm because females can effectively resist being inseminated by extrapair males. Only detailed observations of the nature of extrapair copulations and their success in sperm transfer can discriminate between these alternatives.

In this study we combined analyses of copulation behaviour and parentage of a highly colonial seabird, the little auk, to investigate the functional significance of extrapair copulations in this species and the behavioural role of the sexes in this context. This high-Arctic bird species is a typical seabird with long-term pair bonds and a socially monogamous breeding system. High and coordinated parental investment of both sexes in rearing a single chick annually is required (Harding et al. 2004). A few studies of the breeding behaviour of little auks have been conducted (Evans 1981; Stempniewicz 2001), but the copulation behaviour has not been studied in any detail. A previous molecular paternity study (Lifjeld et al. 2005), conducted in the same colony as the present study, reported no cases of extrapair paternity in a small sample of 26 chicks. We analysed a larger sample of chicks to improve the estimate of the extrapair paternity frequency in the species and make a better comparison of the frequencies of extrapair copulation and extrapair paternity.

METHODS

Field Activity

We studied little auks in the breeding colony at Ariekammen slopes (77°00′N, 15°33′E) in Hornsund (South Spitsbergen) during the breeding seasons of 2004, 2005 and 2006. Ringing and blood sampling of adults and chicks were carried out in all 3 years, whereas studies of copulation behaviour were carried out in 2005 and 2006. For detailed monitoring of copulation behaviour, birds were caught in mist nets or nooses spread on the colony surface and marked individually (with colour rings and signs painted on the breast feathers with the dye Vogelfarbe, Ciba-Geigy, Basel, Switzerland). A 25 μl blood sample was taken from the brachial vein for genetic sex identification. All birds were in adult plumage (ie. 2 years or older; distinguished from subadults by the appearance of flight feathers and upper wing coverts; Stempniewicz 2001). We selected 10 pairs in 2005 and 21 pairs in 2006 in which both mates were marked individually. Social pairs could easily be recognized, as pair mates stay close together continuously in the prelaying period. Their status was also confirmed later in the breeding season when they were observed incubating and rearing a chick in the same nest. As all marked birds were breeding in close proximity to each other, two observers could simultaneously observe all marked birds present in the colony at a given time.

As little auk nests are often inaccessible under rocks and boulders, the exact egg-laying dates of the observed pairs were usually not known. Therefore, the timing of egg laying in the study colony was determined by day-to-day examination of a group of 28 nests in 2005 and 67 nests in 2006. The period before the first egg appeared in inspected nests was defined as the prelaying period. The egg-laying period lasted until the last egg was laid in the group of inspected nests. In both seasons egg laying was highly synchronous; all eggs were laid within 7 days in 2005 and 6 days in 2006.

Observations of marked birds started 6 (10 June) and 10 days (31 May) before egg laying commenced in 2005 and 2006, respectively, and were continued until the end of the egg-laying period. This was the peak of the little auks' copulation activity in the colony (Fig. 1). Observations were made usually in 1–12 h sessions between 0900 and 2300 hours. In total, we collected 137 h of observations (47 h in 2005 and 90 h in 2006), which corresponds to a mean ± SE of 11.6 ± 1.6 h and 27.6 ± 0.9 h for individual birds in 2005 and 2006, respectively. As females spent less time in the colony than males, the total observation time for pair mates together was 9.6 ± 2.2 h in 2005 and 16.1 ± 2.0 h in 2006.

During each hour of observation, we noted the presence of individually marked birds in the colony (checked every 10 min) and their copulation activity. For all records of copulations their success rate (i.e. whether cloacal contact was achieved or not) and the partner category (pair or extrapair mate) were determined. Copulations between pair mates were classified as within-pair copulations. All other copulations were classified as extrapair copulations. A copulation was considered successful when the male mounted the female with both feet placed on her back, moved his tail from side to side and achieved at least one cloacal contact. In cases where it was not possible to see directly whether cloacal contact was achieved, we used mounting duration and female behaviour to indicate copulation success. Unsuccessful copulations were short, often without female cooperation (she raised her body in an upright position and thereby prevented the male from sitting on her back).

As a background for copulation watches of marked birds, we surveyed copulation activity among unmarked birds from 31 May to 7 July 2005 (from the 16th day before the onset of egg laying to the 23rd day of the incubation period) and from 16 May to 19 July 2006 (from the 25th day before the onset of egg laying to the 12th day of the chick-rearing periods; Fig. 1). All occurrences of mounting (including accepted and forced copulations) were noted during a 5 min period in an area of 900 m^2 with nests of ca.300 pairs and with ca.200–300 birds observed during each count. We carried out up to five 5 min watches at different hours during a day to avoid a potential influence of time of day on birds' activity. In 2005, we did 50 counts and in 2006, 151 counts.

Blood samples (25 μl) for parentage and sex identification were collected from 14, 14 and 36 families (two parents and offspring) in 2004, 2005 and 2006, respectively. Among the 64 families, three pairs of parents were included in the genetic analyses in all 3 study years, and four pairs in 2 of the study years. In addition, two parents were included in 2 study years, but they bred with different partners. Only two pairs from 2005 and four pairs from 2006 were included in both the genetic analyses and the copulation watches. Parent birds were caught during the incubation period and marked individually. Observations during the incubation and chick-rearing periods confirmed that the correct parents had been caught at each nest. Among the 64 eggs laid, two did not hatch. A tissue sample of the dead embryos was collected and preserved in 96% ethanol. The remaining 62 eggs hatched successfully and we took a blood sample from chicks at the age of 1–3 weeks. The blood sample (25 μl) was taken from the brachial vein and stored in 1 ml of lysis buffer.

Laboratory Analyses

We extracted DNA from 100 μl of blood and buffer solution, using the Blood Mini kit (A&A Biotechnology, Gdynia, Poland), for molecular sex identification. These analyses were carried out at the University of Gdańsk, Poland. The protocol was optimized to amplify introns on the *CHD-W* and *CDH-Z* genes located on the avian sex chromosomes (Z and W) using the primer pair 2550F and 2718R described by Fridolfsson & Ellegren (1999). Agarose gel electrophoresis revealed one band (i.e. ZZ) in the male and two bands (i.e. ZW) in the female.

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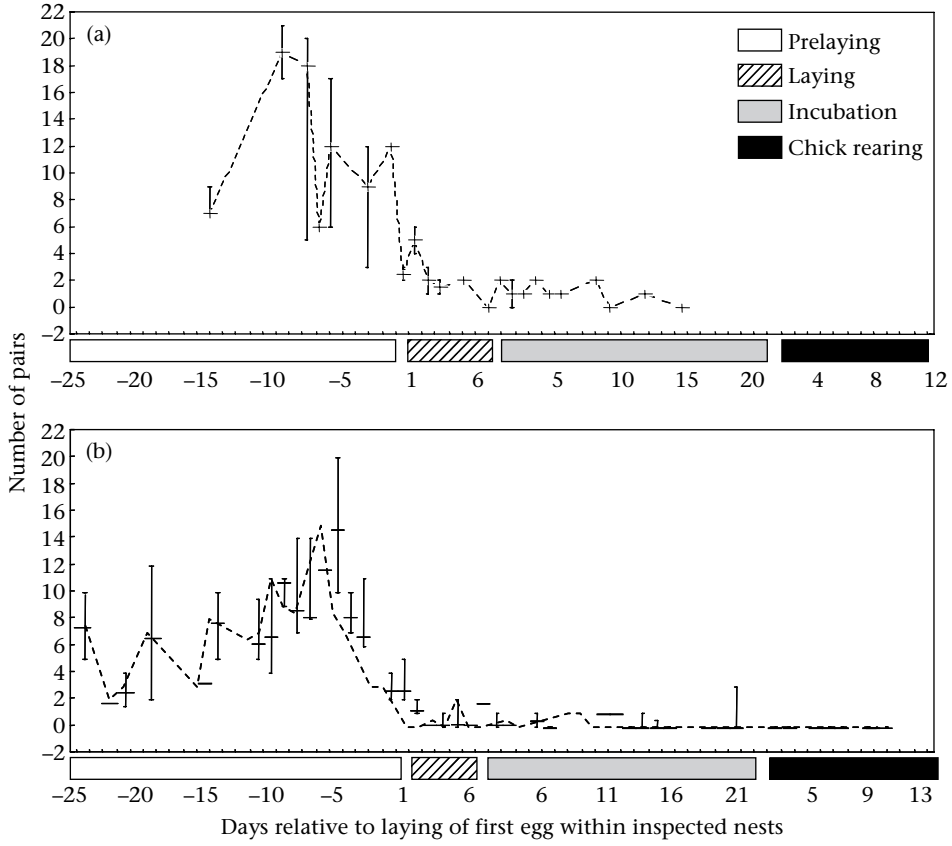

Figure 1. Numbers of unmarked little auk pairs observed copulating during 5 min of 'scanning' the surface of the colony patch (ca.300 breeding pairs) on particular days in the (a) 2005 and (b) 2006 breeding seasons. Medians are shown with 25–75% quartiles.

The parentage analyses were carried out at the Natural History Museum, University of Oslo, Norway, based on DNA extracted with the E.Z.N.A. Blood DNA or Tissue DNA kits (Omega Bio-Tek, Inc, Doraville, GA, U.S.A.) following the manufacturer's protocol. The parentage analyses followed the procedure described in Lifjeld et al. (2005), using the three microsatellite markers Apy03, Apy08 and Apy14 originally developed from the whiskered auklet, *Aethia pygmaea* (Dawson et al. 2005). These three markers are hypervariable in the little auk and make a powerful paternity testing system with an average exclusion probability of 0.998 with one parent known (Table 1). In a few cases of allelic mismatches, families were analysed with one or two extra microsatellites (Apy06 and Apy09; Dawson et al. 2005) to increase the exclusionary power. Parentage and various parameters of marker polymorphism were analysed with CERVUS 3.0 (Kalinowski et al. 2007). Details of marker polymorphism are presented in Table 1 for all five loci.

Descriptive statistics are expressed as mean and ±SE or median and 25% (Q_1) and 75% (Q_3) quartiles.

Ethical Note

All birds were handled with permission from the Norwegian Animal Research Authority and the Governor of Svalbard. Blood sampling did not appear to have any detrimental effect on handled birds. All of them were released unharmed after 5–10 min of handling.

RESULTS

Copulation Behaviour

Among marked birds, 756 copulations were observed during the last few days of the prelaying period over the two seasons. Of these,

Table 1
Polymorphism data for five microsatellite markers in the little auk

Parameter	Microsatellite locus					Combined values	
	Apy03	Apy08	Apy14	Apy06	Apy09	Three loci	Five loci
No. of adults genotyped	108	106	108	20	12		
No. of alleles	24	47	55	13	21	42.0	32.0
Size range (base pairs)	158–229	106–212	216–300	153–213	183–264		
Expected heterozygosity	0.908	0.961	0.928	0.906	0.986	0.932	0.938
Observed heterozygosity	0.889	0.962	0.852	1.0	1.0		
Polymorphic information content	0.896	0.955	0.921	0.873	0.942	0.924	0.918
Estimated null allele frequency	0.007	−0.003	0.043	−0.063	−0.029		
Exclusion probability (first parent)	0.675	0.840	0.752	0.619	0.799	0.987	0.9990
Exclusion probability (second parent)	0.806	0.913	0.857	0.765	0.888	0.998	0.9999

The microsatellite loci and their primer sequences are described in Dawson et al. (2005). Values were calculated using CERVUS 3.0 (Kalinowski et al. 2007).

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24% were extrapair copulations. Involvement in extrapair copulations was recorded for 75% of all marked individuals in 2005 (Six males and nine females in the 10 pairs) and 81% in 2006 (17 males and 17 females in the 21 pairs). For these birds, extrapair copulations made up on average 14.3 ± 1.8%, of all copulation attempts for the 23 males and 17.1 ± 2.9% for the 26 females.

Extrapair copulations were generally unsuccessful. Of the 179 extrapair copulations observed, 168 (i.e. 94%) were forced by the male and ended with the female flying away before cloacal contact could be achieved. Only 11 extrapair copulations were performed with female acceptance; however, three of them also ended without cloacal contact. Thus, only eight (4%, $N = 179$) cases of successful extrapair copulations were noted. These were recorded in the period from 4 days before the start of egg laying until the fourth day of egg laying. The eight successful extrapair copulations made up only 2% of all copulations with cloacal contact observed ($N = 330$) among the study pairs. They were performed by eight different individuals three females and five males, and in all cases with an unmarked partner. No successful extrapair copulations were recorded for the six females that were also included in the parentage analysis and none of them produced extrapair offspring.

The within-pair copulation rate was 1.1 ± 0.2 copulations/h of the mates' shared presence in the colony in 2005 ($N = 10$ pairs) and 0.7 ± 0.1 in 2006 ($N = 21$ pairs). The frequency of within-pair copulations differed significantly between seasons (t test: $t_{29} = -2.43$, $P < 0.05$). The success rate of within-pair copulations was similar in the 2 study years (2005: $\overline{X} \pm \mathrm{SE} = 57.6 \pm 7.6\%$, $N = 10$ pairs; 2006: $55.9 \pm 4.7\%$, $N = 21$ pairs; t test: $t_{29} = 0.21$, $P = 0.83$). The success rate of within-pair copulations of the 26 individual females that engaged in extrapair copulations was significantly higher than the success rate of their extrapair contacts ($\overline{X} \pm \mathrm{SE} = 55.8 \pm 4.7\%$ versus $4.2 \pm 1.9\%$; Wilcoxon signed-ranks test: $Z = 4.32$, $N = 26$, $P < 0.001$).

Parentage Results

In 57 of the 64 analysed families, the chick's genotype at the three main microsatellite loci (Apy03, Apy08, Apy14) made a complete match with the genotypes of the social parents, and we thus concluded that all these 57 chicks were true descendants of their social parents. For the seven remaining chicks there were mismatches at one or more loci with either or both parents, and these cases were evaluated in more detail for possible parentage exclusion for one or both parents.

Two chicks, raised by the same set of parents (in 2005 and 2006, respectively), had a single mismatch with the father at one locus (Apy14). Both chicks had a paternal allele of 251 bp, whereas the father was apparently homozygous for the 249 bp allele. Since both chicks matched the father at the other four loci, we concluded that the mismatched allele was due to an allelic dropout, and that the father sired both chicks. Similarly, a case of allelic dropout might also explain a single mismatch at Apy14 in a third chick, in which the mother was apparently homozygous for a 225 bp allele, and the chick had a 223 bp allele lacking in both parents. Alternatively, the mismatched allele could have arisen from mutation. The probability of random inclusion of maternal alleles at the other loci was 0.00044. We conclude that this chick was also a true descendant of its parents.

In two families, the chick had several mismatches with both parents. One of them did not match any parental alleles at any of the five loci. The other had four allelic mismatches at four different loci: two maternal mismatches, one paternal mismatch and one undecided (similar parental alleles). We concluded that both chicks were genetically unrelated to both parents. The two remaining chicks had a complete genotype match with the mother but mismatched the father at three and five loci, respectively. We excluded the social father as sire in these cases.

In summary, the parentage analyses revealed that 60 of the 64 chicks were legitimate offspring of the social parents, two were unrelated to the father, and two were unrelated to both parents. We concluded that two of 62 chicks were sired through extrapair fertilization. This corresponds to a rate of 3% extrapair paternity with a 95% confidence interval of 0.39–10.44%, calculated according to Rohlf & Sokal (1981).

DISCUSSION

Little auks engaged in extrapair copulations with a frequency higher than expected from the low occurrence of extrapair paternity. Around a quarter of all copulation attempts involved extrapair partners and more than half of all study individuals engaged in one or more extrapair copulation events. A high occurrence of extrapair copulations has also been reported for some other ecologically similar seabird species such as the razorbill, *Alca torda* (96% of females were involved in extrapair copulations; Wagner 1992a) and northern fulmar, *Fulmarus glacialis* (16% of females; Hunter et al. 1992).

However, a great majority of extrapair copulations (94%) in little auks were unsuccessful in terms of cloacal contacts not being achieved. Hence, only 2% (8/330) of all copulations with cloacal contact, and thus presumably sperm transfer, were extrapair copulations. The proportion makes a fairly good match with the actual frequency of extrapair paternity in the population. We found 3% extrapair offspring, but if we include the previous study of Lifjeld et al. (2005) with no record of extrapair paternity among 26 chicks, the combined estimate of extrapair paternity in the population is 2%. This suggests that the occurrence of extrapair fertilization is proportional to the relative share of extrapair copulation in the total sperm transfer.

Similarly low rates of extrapair paternity as in the little auk have been reported for the closely related common guillemot, *Uria aalge* (8%, $N = 77$; Birkhead et al. 2001) and Brünnich's guillemot, *Uria lomvia* (7%, $N = 27$; Ibarguchi et al. 2004), as well as the Atlantic puffin, *Fratercula arctica*, (0%, $N = 38$, Anker-Nilssen et al. 2008). Copulation data are relatively scarce in these other species, but if the pattern from the little auk is representative of the group as a whole, it seems that the low rate of extrapair paternity is proximately caused by a lack of female interest in engaging in extrapair copulation in these species. However, copulation data have revealed a strong active role of females in initiating extrapair copulations in the razorbill (Wagner 1992a, b), but, unfortunately, the functional significance of this behaviour is hard to assess as paternity data for this species do not exist.

Avoiding extrapair insemination by little auk females may be a consequence of the need for extensive male parental care (Harding et al. 2004; Wojczulanis-Jakubas 2007), and the benefit of long-term pair bonding for reproductive success. Males could withhold parental care or desert if they were cuckolded, which would result in reproductive failure for both mates in the current season. Female infidelity could also lead to mate switching in the next breeding season. Thus female infidelity could be more costly to their current and future reproductive success than any benefits of multiple mating and extrapair fertilization. It is also possible that by avoiding cloacal contact with extrapair partners, females reduce the potential risk of being infected by a sexually transmitted disease. Although knowledge about the functional significance of sexually transmitted diseases is scarce for wild bird populations, numerous species of pathogenic microbes have been isolated from the cloacae of wild birds (Lombardo et al. 1996).

Despite the overall low frequency of successful extrapair copulations, there were a few females who fully accepted extrapair

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copulations and some of these copulations resulted in cloacal contact. Female cooperation during the copulation (allowing mounting and exposing the cloacal mouth) seemed to be crucial for the male to achieve cloacal contact. Hence, females seem to exert behavioural control over extrapair copulations.

It therefore seems plausible that females may gain some reproductive benefits from engaging in a few extrapair copulations or with particular extrapair males, while there might be no net benefits from extrapair copulation at large. One proposed benefit of female extrapair copulation is insurance against their mate's infertility (Wagner 1992b; Lifjeld et al. 2007). If male infertility does occur, but at a low rate, fertility of the egg can be achieved by a single copulation with another male. Hence, the fertility insurance hypothesis can explain the low incidence of successful extrapair copulations and the low rate of extrapair offspring. The fact that females engage in a few extrapair copulations may impose a selection pressure on males to reduce the risk of being cuckolded. The high frequency of within-pair copulations may therefore be regarded as a paternity assurance strategy, to swamp the sperm from extrapair males (Birkhead et al. 1987). From our data on colony attendance and copulation rates during the last 6 and 10 days of the prelaying period, we can estimate an average total of 16 and 32 successful copulations per pair, in the 2 study years, respectively. Comparable estimates are available for the northern fulmar (on average 19 copulations during the prebreeding season; Hunter et al. 1992) and razorbill (50 copulations during the 30 days prior to egg laying; Wagner 1992c). Frequent within-pair copulations may also play a role in the breeding synchronization, which is crucial for breeding success in the short Arctic summer, with frequent gull predation (Stempniewicz 1991, 1995; Wojczulanis et al. 2005). Interseasonal differences in the frequency of within-pair copulations seem to confirm that little auk pairs copulated more frequently in the season with a longer period of snow cover in spring, a factor delaying onset of egg laying in little auks (B. Moe et al. unpublished data).

It is worth noting that two of the 64 chicks analysed did not match either parent at the nest. The possibility exists that they were misidentified, that is they belonged to another set of parents, since their blood was sampled at a relatively late age (2–3 weeks old) and older chicks are mobile and theoretically able to move between nests. Alternatively, the two cases might result from egg dumping or adoption. Eggs might have been dumped by females that copulated successfully but did not have a nest or a partner. If a female can successfully replace a host's egg with her own (we occasionally observed in some nest burrows an extra egg jammed among stones), the host birds might have accepted it as their own and continued to incubate. Guillemots are known to accept a foreign egg if their own is lost (Gaston et al. 1993). At present, we are unable to confirm the origin of these two mismatches, but the potential for adoption of eggs or chicks clearly deserves further study.

In conclusion, our integrated study of copulation behaviour and genetic parentage indicates that the low incidence of extrapair paternity is largely due to female resistance against male-enforced extrapair copulation. This highlights a role for female control of insemination success of copulation attempts. Females seem to resist extrapair copulations in general, but may benefit from engaging in a few extrapair copulations, possibly to ensure fertility of the egg if the male is infertile.

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