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LOW FREQUENCY OF EXTRA-PAIR PATERNITY AND HIGH FREQUENCY OF ADOPTION IN BLACK-LEGGED KITTIWAKES

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Abstract. We studied the timing and frequency of extra-pair copulations and extra-pair fertilizations in the Black-legged Kittiwake (*Rissa tridactyla*), a socially monogamous seabird that breeds in dense colonies. We recorded 313 copulations by 82 marked pairs in 25 000 nest-hr over three years. We recorded only two extra-pair copulations, both of which were obtained by opportunistic males that disrupted pair copulations in progress. Pairs performed a mean of 14 copulations per clutch suggesting that males may copulate relatively frequently for paternity assurance. Our parentage analysis based on eight microsatellite markers did not detect any extra-pair paternity in 119 offspring from 86 broods; however we did detect three cases of adoption caused by chicks moving to adjacent nests. The between-nest movement of a minimum of 8% of chicks suggests that escaping siblicide may be an adaptive strategy for some nestlings, despite the risk of falling into the sea and drowning (observed in 11 of 21 chicks).

Key words: adoption, Black-legged Kittiwake, extra-pair copulation, extra-pair paternity, paternity assurance, Rissa tridactyla*, within-pair copulation.*

Baja Frecuencia de Paternidad Extra-Pareja y
Alta Frecuencia de Adopción en
Rissa tridactyla

Resumen. Estudiamos la frecuencia de cópulas y
fertilizaciones extra-pareja y el momento en que éstas
ocurrieron en *Rissa tridactyla*, un ave marina social-
mente monógama que se reproduce en colonias densas.
Registramos 313 cópulas por parte de 82 parejas mar-
cadas en 25 000 horas-nido a través de tres años. Re-
gistramos sólo dos cópulas extra-pareja, ambas obte-
nidas por machos oportunistas que perturbaron cópulas
que se estaban efectuando entre miembros de una pa-
reja. Las parejas realizaron un promedio de 14 cópulas
por nidada, lo que sugiere que los machos estarían co-
pulando frecuentemente para asegurar su paternidad.
Nuestros análisis basados en ocho marcadores micro-
satélites no detectaron ninguna instancia de paternidad
extra-pareja en 119 crías de 86 nidadas. Sin embargo,
detectamos tres casos de adopción causados por el mo-
vimiento de pichones a nidos adyacentes. El movi-
miento entre nidos de al menos el 8% de los pichones
sugiere que escapar del siblicidio podría ser una estra-
tegia adaptativa para algunos de éstos, a pesar del ries-
go de caer al mar y ahogarse, lo que se observó en 11
de 21 pichones.

During the past two decades, extra-pair copulations
(EPCs) have been shown to be common in socially
monogamous species (Birkhead and Møller 1992, Pe-
trie and Kempenaers 1998, Griffith et al. 2002). Fe-
males may engage in EPCs to acquire indirect benefits
such as good genes (Kempenaers et al. 1992) or ge-
netic diversity (Olsson et al. 1994, Petrie et al. 1998),
or direct benefits such as food (Gray 1997), fertiliza-
tion insurance (Birkhead and Møller 1992, Wagner
1992a) or parental care (Davies et al. 1992). It has also
been suggested that extra-pair copulations are more
frequent in colonial species (Birkhead et al. 1987,
Møller and Birkhead 1993). Colonial breeding pro-
vides opportunities for extra-pair copulations because
there are many easily accessible potential extra-pair
partners (Møller 1987). In addition, males in colonial
species are generally unable to guard their mates be-
cause one partner must defend the nest while the other
partner forages (Birkhead et al. 1987, Birkhead and
Møller 1992). Instead, males in non-mate-guarding
species typically copulate frequently to assure their pa-
ternity (Birkhead et al. 1987, Wagner 1992b, Møller
and Birkhead 1993). Various hypotheses predict that
the level of extra-pair paternity should be negatively
correlated with the degree of paternal investment, the
male reproductive lifespan, and the duration of the pair
bond (Griffith et al. 2002). However, numerous excep-
tions to these generalizations exist, making it desirable
to increase the number of species under investigation.
For example, Waved Albatrosses (*Pheobastria irro-
rata*) and Adélie Penguins (*Pygoscelis adeliae*), de-
spite fitting the profile of species with low extra-pair
paternity, have been reported to have substantial levels
of extra-pair paternity (respectively 25% and 9% of
young are extra-pair, Huyvaert et al. 2000, Pilastro et
al. 2001).

The Black-legged Kittiwake (*Rissa tridactyla*) is a
well-studied pelagic colonial seabird with a monoga-
mous mating system (Coulson and Thomas 1983). Al-
though extra-pair copulation and extra-pair paternity
frequencies are known to be lower in seabirds than in
passerines and other groups (Westneat and Sherman
1997, Birkhead et al. 2001), kittiwakes could be ex-
pected to exhibit at least some level of EPC and extra-
pair paternity for the following reasons. First, kitti-
wakes breed in highly dense colonies (Cramp 1985)
where extra-pair copulation opportunities are numer-
ous. Moreover, as in many species where males feed
their mates prior to egg laying (Birkhead et al. 1987),
female kittiwakes are largely unattended by their mates
during their presumed fertile period when they wait at
the nest to be fed (Helfenstein 2002, Helfenstein, Wag-
ner et al. 2003). Second, several studies have suggest-
ed that individual kittiwakes vary widely in their in-
trinsic genetic quality (Coulson and Wooller 1976,
Coulson and Thomas 1985, Cam et al. 2002). In this
context, female kittiwakes may be expected to seek
extra-pair copulations from high-quality extra-pair
males to obtain extra-pair fertilizations. Courtship
feeding may lead to increased clutch size (Helfenstein,
Wagner et al. 2003), and female kittiwakes could ac-
crue direct benefits by trading extra-pair copulations
for food as in some other species (Wolf 1975, Gon-
záles-Solís et al. 2001). The primary aim of this study
was to examine the frequencies and seasonal timing of
within-pair and extra-pair copulations and to identify
which individuals might engage in EPCs. We used
eight microsatellite markers (Tirard et al. 2002) to an-
alyze parentage on a set of 86 families, and estimated
the frequency of extra-pair paternity.

Siblicide has been reported in kittiwakes by Dickins
and Clark (1987), and we observed that sibling ag-
gression may lead to heavy injuries and death (Roberts
and Hatch 1994). Our other goal was to document the
occurrence of adoption that may result from nestlings
moving to adjacent nests to escape sibling aggression
(Roberts and Hatch 1994).

METHODS

The study was conducted in Cap-Sizun, Brittany,
France (48°50′N, 4°35′W) from 1999 to 2001. This
kittiwake population has been extensively studied
since 1979, and more than 15 000 individual birds
have been color banded either as chicks or adults
(Danchin and Monnat 1992, Helfenstein, Wagner, et
al. 2003). We observed one cliff comprising more than
250 breeding pairs every year. In this cliff, we focused
on a subsample of 14 nests in 1999, 29 in 2000, and
39 in 2001, in which both males and females were
color banded. The disposition of this open, vertical
cliff allowed us to observe all the nests from a single
observation point approximately 30 m away. We made
observations from the early copulation period (mid-
March) to the end of egg laying (early June). During
daily observation sessions of 1 to 10 hr, we recorded
all copulation attempts involving individuals of the fo-
cal pairs. Copulations were classified as successful if
we observed mountings with cloacal contact, or un-
successful if we observed mountings without cloacal

contact. We recorded the identities of the copulating birds or noted when one of them was unmarked.

As part of a broader study on life-history traits in kittiwakes (Danchin and Monnat 1992, Danchin et al. 1998, Cam et al. 2002), we also monitored the entire colony daily. We scanned all nests and recorded the laying date of the first egg, the number of eggs laid, and the number of chicks hatched. During the monitoring routine, we were able to observe occasions when a chick moved from its nest to an adjacent one. All means are reported ± SD.

BLOOD SAMPLING AND GENETICS

In addition to behavioral observations, we collected blood samples from chicks (ca. 0.2 mL) and adults (ca. 0.4 mL) for subsequent DNA extraction and genotyping. Blood was collected from the brachial vein and stored in Tris-EDTA. Chicks were sampled during banding, when they were 8 to 25 days old. For all nests, the complete brood (1.5 ± 0.6 chicks, range 1–3 chicks, n = 86 families) was sampled. Adults were caught on the nest using a metal hook fixed at the end of a 4-m fishing rod. Microsatellite genotypes were obtained from each individual at seven loci developed from kittiwakes (Tirard et al. 2002) and one locus developed from Common Murres (*Uria aalge*; Ibarguchi et al. 2000). DNA extractions, PCR amplifications, and profiles were obtained using the method described in Tirard et al. (2002). All genotypic profiles were scored by CT.

RESULTS

BEHAVIORAL DATA

We observed 313 successful copulations involving 52 marked males and 56 marked females in three years and 800 hr of observation (223 hr in 1999, 67 hr in 2000 and 512 hr in 2001, a total of ca. 25 000 nest-hr). The vast majority of the copulations (90%) occurred between 21 days before and 2 days after the laying of the first egg (day 0) and peaked at day −5 (Fig. 1). The remaining 37 copulations occurred earlier, between days −54 and −23. Copulation rate began to increase at 21 days before laying (Fig. 1), which was also the mean starting date of the pairs' nest-building activity (Helfenstein, Wagner, et al. 2003). Nest building requires coordination between partners and occurs after pair formation (Cam et al. 1998, Helfenstein, Wagner, et al. 2003). We therefore considered only copulations occurring between days −21 and +2 to be postpairing copulations. The mean sperm storage duration in birds varies widely (Birkhead and Møller 1992). The amount of time that female kittiwakes can store sperm is not known, but we conservatively assumed that any sperm transferred between 21 days before and 2 days after laying may fertilize the eggs. Mean copulation frequency in this period was 0.04 ± 0.03 copulations hr^{-1} which totals 14.1 ± 10.6 copulations per clutch (n = 79 pair-years) on a 14-hr daylight basis. Of 394 copulation attempts (comprising both successful and unsuccessful copulations) six (1.5%) were EPC attempts. Three unsuccessful EPC attempts were made by the same male with the same female in one year. We observed two successful extra-pair copulations, which represents <1% of the 313 suc-
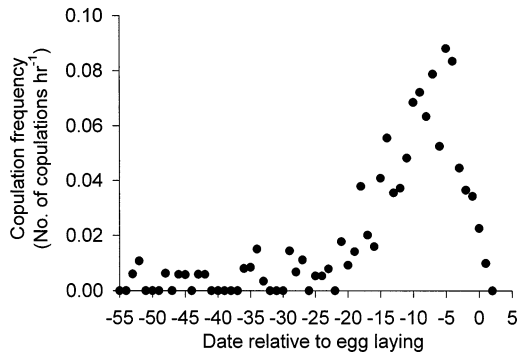

FIGURE 1.   Seasonal variation in copulation frequency in Black-legged Kittiwakes. Copulation frequency is the mean number of copulations per hour per pair. It was computed from observation of 47.0 ± 16.6 pairs per day and is reported relative to the first day of egg laying for each pair (day 0). Copulations commenced more than 50 days before the laying of the first egg of the pair but remained very low until day −21 and peaked on day −5. No copulations were observed more than 2 days after the laying of the first egg.

cessful copulations. All six EPC attempts were initiated by the extra-pair male flying to the female. Males either forcibly mounted the female or disrupted a copulation in progress by displacing the pair male. After disrupting the copulations, extra-pair males were able to replace the resident males on the females' backs and one extra-pair male eventually achieved cloacal contact. The second successful EPC was initiated by a neighboring male that was attending a first-time-breeding female's nest. Successful and unsuccessful EPCs were performed between −17 and −3 days before egg laying (mean 9.7 ± 5.5 days). The two successful EPCs occurred at days −9 and −3.

During our routine daily observation of the colony we observed that, in multiple-chick broods, the first-hatched chicks were often very aggressive toward their younger siblings and repeatedly attacked them with their bills. Younger chicks sometimes tried to avoid sibling aggression by walking into an adjacent nest, but often (11 of 21 chicks) missed and fell into the sea where they drowned. In some cases however, the escaping chicks reached the neighboring nest and were accepted and fed by the adults even when they were still incubating their own eggs. Overall, 10 adoptions occurred in 76 nests of color-banded pairs comprising 119 chicks, which is nearly identical to the 8% adoption frequency found by Roberts and Hatch (1994) in an Alaskan population.

PARENTAGE ANALYSES

Exclusion probabilities were calculated for each marker (Jamieson 1994) based on allele frequency from samples of 63–97 presumably unrelated adults. The combined exclusion probability for the set of 8 markers was 0.98 (range 0.15–0.78). A total of 45 putative fathers, 50 putative mothers, and 119 chicks out of 86 families were genotyped and analyzed. We obtained both behavioral records and genotypic profiles for 25

TABLE 1.   Genotypic composition of the five mismatched sets of putative parents and offspring from a total sample of 86 Black-legged Kittiwake families and 119 chicks. Each letter represents a unique allele at a given microsatellite locus. The probability of false inclusion corresponds to the probability that the parent's genotype can match the offspring's by chance (Jeffreys et al. 1992). Table entries in boldface highlight the loci at which the chick's genotype did not match the genotype of one or both putative parents. Loci are named according to Ibarguchi et al. (2000) and Tirard et al. (2002). Two of three chicks in which microsatellite data indicated adoption were observed moving between nests prior to sampling.

Family	Individual	Locus								Probability of false inclusion	Interpre-tation
		K6	K16	K31	K32	K56	K67	K71	Ulo-12a12		
1	Putative father	**E/E**	A/C	A/C	F/H		A/B	**A/A**	A/B	0.02	
	Putative mother	**E/E**	A/A	A/A	F/G		B/B	**A/A**	A/A	0.12	Adoption
	Offspring	**C/F**	A/C	A/C	F/H		B/B	**B/B**	A/B		
2	Putative father		A/B	**C/C**	**D/G**	A/B	B/B	B/B	A/B	0.06	
	Putative mother		C/C	**C/E**	**D/E**		A/B	A/B	A/B	0.35	Adoption
	Offspring		A/C	**A/D**	**A/G**	A/B	B/B	B/B	A/B		
3	Putative father	**D/E**	**A/B**	C/E	**B/J**		B/B	A/B	A/A	0.05	
	Putative mother	**E/E**	**A/A**	A/C	**A/I**		B/B	A/B	A/B	0.44	Adoption
	Offspring	**A/B**	**A/C**	A/A	**D/J**		B/B	B/B	A/A		
4	Putative father	D/E	A/A	A/A	**C/D**		B/B	A/A	A/A	0.26	Mutation or genotyp-ing error
	Putative mother	E/E	A/C	C/E	**C/C**		A/B	A/B	A/A	0.12	
	Offspring	E/E	A/C	A/E	**B/B**		B/B	A/B	A/A		
5	Putative father	**D/E**	**A/C**	**A/C**	G/H	A/A	B/B	A/B	**A/A**	0.02	
	Putative mother	**B/F**	**A/A**	**A/B**	G/G	A/B	A/B	A/B	**A/B**	0.06	Undeter-mined
	Offspring	**D/E**	**A/B**	**A/E**	G/G	A/A	B/B	A/B	**B/B**		

pairs. Out of the 119 chicks of the genetic sample, 114 had no mismatching alleles in any loci with either the putative mother or the putative father. The average paternal probability of false inclusion (i.e., the probability that the genotype of the putative father matched the genotype of the offspring by chance, Jeffreys et al. 1992) was 0.04 ± 0.05 (range 0.00011–0.24) for these chicks, indicating that they were likely to have been fathered by the pair male. Based on the mean probability of false inclusion, we estimated that, within a 95% confidence interval and assuming a normal distribution, up to 5% of the 114 chicks could be the result of an undetected extra-pair fertilization.

In one case, both parents were excluded at two different loci (Table 1, family 1). The probability of false inclusion on the remaining loci was 0.02 for the putative father and 0.12 for the putative mother and this chick was considered as an adoption. Two other chicks did not match both putative parents' genotypes at one locus and either the putative mother or the putative father at one other locus (Table 1, family 2, 3). Our observations of chicks moving from their nest to a neighboring one confirmed that these two chicks were adoptions. One chick neither matched the paternal nor the maternal alleles at the same single locus (Table 1, family 4). This may be due either to mutation or to adoption. The nest in which the chick had been reared was physically isolated from any other nests, making it impossible that the flightless chick could have transferred itself into a different nest. We therefore considered the mismatches to be due to mutations or genotyping errors. One last chick (Table 1, family 5) did

not match the putative father at one locus and the putative mother at another locus. At two other loci, despite mismatches, shared alleles between parents did not allow us to exclude either the putative father or mother. We were therefore unable to determine the origin of this chick.

For one of the two females that we observed copulating with an extra-pair male, no genetic data were available to analyze the paternity of the offspring. For the other female, the offspring genotype did not show any mismatch with the genotype of the social father. The probability of false inclusion of the social father was quite high (0.07), but no genetic data were available to test the paternity of the putative extra-pair male. Hence, we could not distinguish whether this extra-pair copulation was simply unsuccessful in achieving fertilization or whether we lacked sufficient power to exclude the social father and detect an extra-pair fertilization.

DISCUSSION

Female kittiwakes were never seen seeking extra-pair copulations. In 20 years of population monitoring, copulations have never been observed away from the nesting colonies, making it unlikely that EPCs are performed in other locations (J.-Y. Monnat, unpubl. data). Consistent with these behavioral observations, our genetic analysis did not detect any extra-pair paternity. Our 4% probability of false inclusion does not allow us to conclude that extra-pair paternity is absent in kittiwakes. However, our markers did allow us to detect cases of adoption that had been verified by direct

observations. This latter result, combined with our large sample size of 119 offspring, suggests that if extra-pair paternity is not absent in kittiwakes it is likely to be close to zero.

It is now well established that extra-pair copulations and paternity are common in socially monogamous species (Birkhead and Møller 1992, Petrie and Kempenaers 1998, Griffith et al. 2002). Therefore, as Griffith et al. (2002:2195) have noted, ''levels of extra-pair paternity below 5% of offspring are now considered worthy of explanation.'' Seabirds and many other non-passerines with high levels of paternal care generally exhibit low frequencies of extra-pair paternity (Birkhead et al. 2001). In kittiwakes, biparental care is crucial, and males and females share equally in nest building, incubation, and chick feeding (Coulson and Wooller 1984, Coulson and Porter 1985, Coulson and Johnson 1993, Roberts and Hatch 1993). It has been proposed that a female's decision to engage in extra-pair copulations depends on the balance between the benefits of this reproductive strategy and the costs of male responses to cuckoldry (Birkhead and Møller 1996, Gowaty 1996). Moreover, two comparative analyses (Møller 2000, Møller and Cuervo 2000) have found that the frequency of extra-pair paternity was negatively related to male parental care and to reduction in female reproductive success caused by the removal of the mate. This suggests that high levels of paternity confidence may be a prerequisite for paternal care and that the more females depend on their mates to achieve reproductive success the less likely they may be to engage in extra-pair copulations (Trivers 1972, Fitch and Shugart 1984, Xia 1992). Given the high investment of male kittiwakes in their progeny, this hypothesis may explain why female kittiwakes do not seek EPCs. The pursuit of EPCs may also have other costs for females. Females are unlikely to seek EPCs at another male's nest because material from their unattended nest is likely to be stolen, and this can delay reproduction and reduce reproductive success (FH, unpubl. data). Accepting an extra-pair male on the nest may also have a cost. Nest acquisition is often achieved by prospecting and squatting (Danchin 1987, 1988, Cadiou et al. 1994) and the acquisition of the nest by a new male may lead to divorce or dispersal (Chardine 1987, Danchin and Cam 2002). These potential costs to females may explain why only males initiated EPCs.

We observed males forcing EPCs by interrupting a copulation in progress. Interference in copulations by extra-pair males has been observed in another kittiwake population (Chardine 1986) but without being followed by EPC attempts. The presence of males that try to force copulations may create conditions for the evolution of paternity assurance strategies (Helfenstein, Wagner, and Danchin 2003). Males copulate more (14.1 ± 10.6 copulations per clutch) than is likely to be needed to achieve fertilization. They also perform a mean of 3.4 ± 1.8 ($n = 82$ pairs) cloacal contacts during a single copulation, which leads to an average of 47.6 cloacal contacts performed per clutch. Not all cloacal contacts result in sperm transfer (Hunter et al. 1996) and we cannot exclude the hypothesis that relatively frequent copulation with multiple cloacal con-tacts may have other functions, such as strengthening the pair bond (Wagner 1996, 2003). However, this high number of cloacal contacts may also indicate that males inseminate their mates with more sperm than is necessary if their paternity were not at all at risk (Birkhead et al. 1987). Within-pair copulations reached a peak in frequency five days before egg laying, suggesting that copulations were timed to match female fertility (Birkhead et al. 1987). All these factors combined (cost of retaliation, direct cost of EPCs, paternity assurance strategies) might explain the low level of EPCs and extra-pair fertilizations in kittiwakes.

The behavior of flightless chicks leaving their nests, apparently to seek adoption in a neighboring nest, may occur when the risk of travel between nests (falling into the sea) is lower than the risk of starvation or siblicide. This intriguing phenomenon, reported in several species (Holley 1981, Carter and Spear 1986, Plissner and Gowaty 1988, Morris et al. 1991), raises the question of why parents have not evolved recognition cues or simply forbid access to their nests to outside offspring. A high degree of relatedness between foster parents and the neighboring chicks could explain why individuals adopt stray chicks. Close relatedness could either be due to a high level of natal philopatry or a high level of EPC between neighbors. On the basis of our observations and paternity analysis, we can at least exclude the hypothesis that EPC rate between neighbors is promoting adoption in our study species.

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