



Forced copulation results in few extrapair fertilizations in Ross's and lesser snow geese

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Extrapair paternity varies from 0 to over 70% of young among various populations of birds. Comparative studies have suggested that this variation is related to nesting density, breeding synchrony and the proportion of extrapair copulations. We used minisatellite DNA fingerprinting to examine levels of extrapair paternity in Ross's geese, *Chen rossii*, and lesser snow geese, *C. caerulescens* c. (hereafter snow geese) nesting in the largest known goose colony in the world. These geese have one of the highest known percentages of extrapair copulation (46–56% of all attempted copulations), and all of these appeared to be forced. Among all successful copulations, 33 and 38% were extrapair in Ross's and snow geese, respectively. Despite the high percentage of extrapair copulations, extrapair paternity was low in both Ross's and snow geese (2–5% of young). Extrapair paternity was not related to nest density in either species. However, in snow geese, extrapair paternity was more likely to occur in nests of females that nested asynchronously, either early or late in the season. This is one of a few reported examples of a negative relationship between extrapair paternity and breeding synchrony. Extrapair young also tended to come from eggs laid later in the clutch. Although forced extrapair copulations appear to be a relatively inefficient reproductive tactic for males, they may provide a reproductive advantage for some males.

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In many species of monogamous birds, social pair bonds are not reliable indicators of genetic patterns of mating. Most discrepancies occur when young are sired by males on other territories as a result of extrapair copulations. Less frequently, they occur when females lay their eggs in the nests of other females (intraspecific brood parasitism or egg dumping). The proportion of extrapair young in a population (extrapair paternity) varies from 0 to more than 70% (Gowaty 1996). Extrapair paternity may increase the variance in male mating success and, thus, have an important influence on sexual selection (Webster et al. 1995). To date, little is known about behavioural and ecological factors that influence interspecific vari-

ation in extrapair paternity. Comparative analyses suggest that several factors influence extrapair paternity, including levels of mate guarding and extrapair copulation (Birkhead & Møller 1992), breeding synchrony (Birkhead & Møller 1992; Stutchbury & Morton 1995), breeding density (Møller & Birkhead 1993; but see Westneat & Sherman 1997), and rates of mate switching ('divorce': Cezilly & Nager 1995). Field studies have begun to examine these factors using experiments (e.g. Lifjeld & Robertson 1992) and natural variation within and between populations (e.g. Dunn et al. 1994; Weatherhead 1997).

Until recently, ecological and behavioural explanations for variation in extrapair paternity have focused on the interests of males (reviewed by Lifjeld et al. 1994). For example, it was suggested that greater breeding density would increase the opportunity for males to encounter potential mates, and to gain extrapair copulations and, thereby, extrapair fertilizations (Birkhead & Møller 1992; Møller & Birkhead 1993). Accordingly, extrapair paternity may be more common in colonial than in solitary nesting species and at higher breeding densities within species (Birkhead & Møller 1992; Møller & Birkhead 1993). Low

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synchrony of nesting also may increase opportunities for males to gain extrapair fertilizations (Birkhead & Møller 1992). If males wait until after their own mates are fertile before seeking extrapair copulations, then asynchronous nesting leads to a longer breeding season and more potential extrapair mates for males that breed early.

On the other hand, if fertilization success of males is influenced to a greater extent by females than by males (female 'control'; e.g. Wagner 1991; Lifjeld et al. 1994), then patterns of extrapair paternity may be explained by advantages to females rather than to males. In this case, breeding at greater density or lower synchrony may not increase the benefits of extrapair paternity to females (Dunn et al. 1994) because adding more potential mates will not necessarily increase opportunities for extrapair matings by females, at least above a minimum level of density or synchrony (see also Westneat et al. 1990). Recently, however, Stutchbury & Morton (1995) and Stutchbury & Neudorf (1998) argued that if increased synchrony facilitates the choice of extrapair mates by females, then extrapair paternity should increase as breeding becomes more synchronous. They suggest that greater synchrony increases the number of males attempting to gain extrapair copulations at any given time, and that this increases male–male competition and allows for more accurate assessment of male quality by females, similar to what occurs on a lek (Stutchbury & Neudorf 1998). Thus, depending on assumptions about which sex controls fertilization and whether females gain fitness benefits from changes in synchrony, the level of extrapair paternity may decrease (Birkhead & Møller 1992), stay the same (Dunn et al. 1994) or increase (Stutchbury & Neudorf 1998) with greater breeding synchrony.

As noted above, hypotheses about patterns of paternity often rely on whether females benefit from extrapair fertilizations. It is difficult to test these hypotheses because there are few situations in which it is clear that females of a given species would or would not benefit from an extrapair fertilization. One exception may be 'forced' extrapair copulations, which are relatively common in waterfowl (reviewed by McKinney et al. 1983; McKinney & Evarts 1998). Surprisingly little is known about the fertilization success of extrapair copulations in situations where females appear to resist copulation (i.e. 'forced' copulation) and presumably incur costs. Costs to females may include physical injury, young with genotypes of poorer quality, or reduced male parental care; however, none of these potential costs has been studied rigorously (reviewed by McKinney & Evarts 1998).

We examined extrapair paternity in a sympatric population of lesser snow geese, *Chen caerulescens c.* (hereafter snow geese) and Ross's geese, *Chen rossii*, in the largest known nesting colony in the world. These geese have some of the highest known frequencies of forced extrapair copulation and they breed at high density and synchrony. Thus, they provide an opportunity to examine the relative fertilization success of forced extrapair copulations and to study extrapair paternity in two closely related species under extreme ecological conditions.

METHODS

Study Area

We conducted field work from 6 to 24 June 1993 and 2 June to 6 July 1995 at Karrak Lake (67°14'N, 100°16'W), in the Queen Maud Gulf Bird Sanctuary, approximately 315 km southeast of Cambridge Bay, Nunavut (formerly part of the Northwest Territories), Canada. The Karrak Lake colony is the largest known goose colony in the world, numbering 291 000 Ross's and 297 000 snow geese in 1996 (Alisauskas et al. 1998).

Observations of Copulations

We made systematic observations of within-pair and extrapair copulations of focal pairs of geese in 1993. In 1995, we concentrated on collecting blood samples for parentage analysis, so copulations were recorded ad libitum during the course of other field work. We recorded a copulation attempt when a male attempted to mount and grab the nape of a female. Copulations were recorded as successful when a male appeared to make cloacal contact with the female (tail of male was twisted underneath that of the female and thrust towards her); the success of copulations was noted only in 1993. In 1993, our focal observations were made throughout the 24-h daylight cycle in 4-h time blocks. Time blocks were sampled randomly by each of two observers without replacement, such that all time blocks were sampled every 3 days. Within a time block, each observer completed 16 10-min sampling periods (2.7 h). We attempted to alternate the species of geese under observation such that eight 10-min samples were completed on each species. This scheme of alternating species was not possible in the first few days of the study because of the slightly later arrival of Ross's geese. We also terminated observations on snow geese earlier because of their slightly earlier nesting schedule (see below). Pairs of geese were chosen for observation by pointing spotting scopes into an area that contained approximately 5000 pairs of geese. Following completion of the first sample period, the scope was moved to the right until a pair of the next species to be observed was located. This process was repeated until sampling was completed for the time block. We changed observation locations after each 4-h time block (and each day) to avoid repeated observations of the same pairs.

In 1993 and 1995, we summarized copulation data separately for each species and stage of reproduction. Stages of reproduction were estimated from random samples of the entire population (Table 1), as we did not make observations of individually marked pairs with known nesting chronologies. Stages of reproduction were: (1) 'prelaying', the period from first arrival to the day before mean first egg date; (2) 'laying', the period from mean first egg date to the day before mean clutch completion date; and (3) 'early incubation', the period from mean clutch completion date to the mean of the eighth day of incubation. Logistic regression (SAS Institute 1995) was used to determine whether the probability of observing a copulation during an observation session

(no=0, yes=1) differed between species, while controlling for date and stage of reproduction.

Nesting Density and Synchrony

In 1995, nest density was estimated by counting the number of goose nests within a 20-m radius of each nest sampled for parentage. We identified the species occupying each nest by direct observation or by egg size (Alisauskas et al. 1998). Nests chosen for parentage analysis were selected randomly by finding the nest closest to a random point on transects throughout the colony. All nests in the parentage analysis were located after one or two eggs were laid, and, thus, laying date of the first egg was estimated by backdating, assuming one egg was laid every 1.3 days (LeSchack et al. 1998). Nests were visited every 3–5 days to determine clutch size and hatching date. Eggs become discoloured with age (Cooke et al. 1995; A. Afton, unpublished data), so laying order of eggs was determined by numbering new eggs laid between nest visits according to the amount of staining on each egg (if more than one new egg was laid). This method was completely accurate when tested on a subsample of nests visited every other day (A. Afton, unpublished data). We calculated an index of breeding synchrony (Bjorklund & Westman 1986; Kempenaers 1993) that gives the average percentage of females that are fertile on any given day during the entire fertile period of the population. The fertile period of wild geese is unknown; however, captive studies of other species indicate that females are fertile at least 5 days before the first egg (Kempenaers 1993). Thus, for each female, we used a fertile period that started 5 days before the first egg was laid and ended on the day the penultimate egg was laid.

DNA Fingerprinting

We conducted DNA fingerprinting of 23 families of snow geese and 27 families of Ross's geese. Adult geese were captured with bow-net traps or mist nets; some adult males were shot for other studies (see LeSchack et al. 1998). DNA was extracted from whole blood (100–200 μ l) that was collected from a puncture in the brachial (captured adults) or tarsal (goslings) vein or heart (collected adult males) and stored in lysis buffer (Seutin et al. 1991) at 4°C prior to analysis. Blood was collected from young while they were still in eggs (during web-tagging) to exclude potential mismatches caused by brood mixing after hatch. We used standard techniques of multilocus DNA fingerprinting to analyse our families (e.g. Lifjeld et al. 1993). Briefly, *Hae* III was used to digest the DNA, which was then subjected to electrophoresis (6 μ g of DNA per lane) and Southern blotted onto Hybond N+ transfer membranes. All membranes were probed with *per* (Shin et al. 1985) and then autoradiographed. One membrane was reprobbed with M13 (Vassart et al. 1989) to increase the total number of bands scored for each individual. On average, 20.0 (range 15–31) and 15.7 (range 12–25) bands were scored for Ross's and snow geese, respectively.

Parentage analysis

We used presence of novel fragments and band sharing to determine parentage (Westneat 1990). Novel fragments are fingerprint bands of nestlings that are not found in either parent. If a nestling is the true descendant of two parents, then it will inherit all of its bands from those parents, barring any mutation. Mutation rates for minisatellite DNA are in the order of one to five per 1000 meiotic events (Burke & Bruford 1987; Westneat 1990), which implies that a few novel fragments may occur in a small proportion of offspring. The probability that a given number of novel fragments arose from mutation can be calculated from the Poisson distribution using the mean number of novel fragments found in offspring (see Burke & Bruford 1987). In our case, the probability that a gosling would have two mutant bands was 0.059, and 0.008 for three mutant bands. Therefore, we excluded young with three or more novel bands as offspring of one or both putative parents. For the excluded young, we used the proportion of bands shared between a gosling and each of its parents (Wetton et al. 1987) to determine which of the two parents (if not both) was unrelated to the gosling. Band sharing between true parents and descendants should average 50% based on Mendelian inheritance, while band sharing between putative parents and young produced by extrapair fertilization or egg dumping should be similar to the background level of band sharing in the population. Thus, we used the distribution of band sharing values between mothers and their unexcluded young to estimate a cutoff (lower 99% one-tailed confidence interval) for band sharing between parents and their direct descendants. This cutoff value did not overlap with the distribution of background band-sharing in the population (see Results).

RESULTS

Nesting Density and Synchrony

Nesting synchrony was high in both species. Ross's and snow geese initiated laying within a range of 16 and 21 days in 1993 and 19 and 22 days in 1995, respectively (population sample; Table 1, Fig. 1). Mean laying date (date of first egg) differed between snow and Ross's geese by 4 days in 1993 and 2 days in 1995 (Table 1). The synchrony index (Kempenaers 1993) was 66.1% for snow geese and 70.3% for Ross's geese (1995 parentage sample). Our index was based on the mean percentage of females that were fertile on any given day during the fertile period of all females in the parentage sample (see Methods). Density of conspecific nests was high, but did not differ between snow (12.5 nests/ha) and Ross's (17.7 nests/ha) geese (parentage sample, Table 1; $t=1.53$, $P=0.13$).

Copulations

Over both years, we saw 45 copulation attempts in snow geese and 20 in Ross's geese (Table 2). Approximately half of these attempts were by extrapair males in both snow (47%, 21/45) and Ross's geese (55%, 11/20).

Table 1. Nesting data for Ross's and snow geese, Karrak Lake, Nunavut, Canada, 1993 and 1995

	Ross's geese						Snow geese					
	1993			1995			1993			1995		
	\bar{X}	SE	N	\bar{X}	SE	N	\bar{X}	SE	N	\bar{X}	SE	N
Population sample												
Laying date	12 June	0.2	262	8 June	0.1	318	8 June	0.2	262	6 June	0.1	396
Clutch size	3.2	0.1	262	3.4	0.1	318	3.6	0.1	262	3.5	0.1	396
Start of incubation	16 June	0.2	262	13 June	0.1	318	13 June	0.1	262	11 June	0.1	396
Parentage sample												
Laying date				9 June	1.8	27				7 June	2	23
Clutch size				3.6	0.6	27				3.7	0.9	23
Start of incubation				13 June	1.9	27				12 June	2.2	23
Nests/ha												
Conspecific				17.7	2.5	27				12.5	2.3	23
Total				22.1	2.7	27				18.7	2.9	23

Nests were chosen randomly for both population and parentage (DNA fingerprinting) samples.

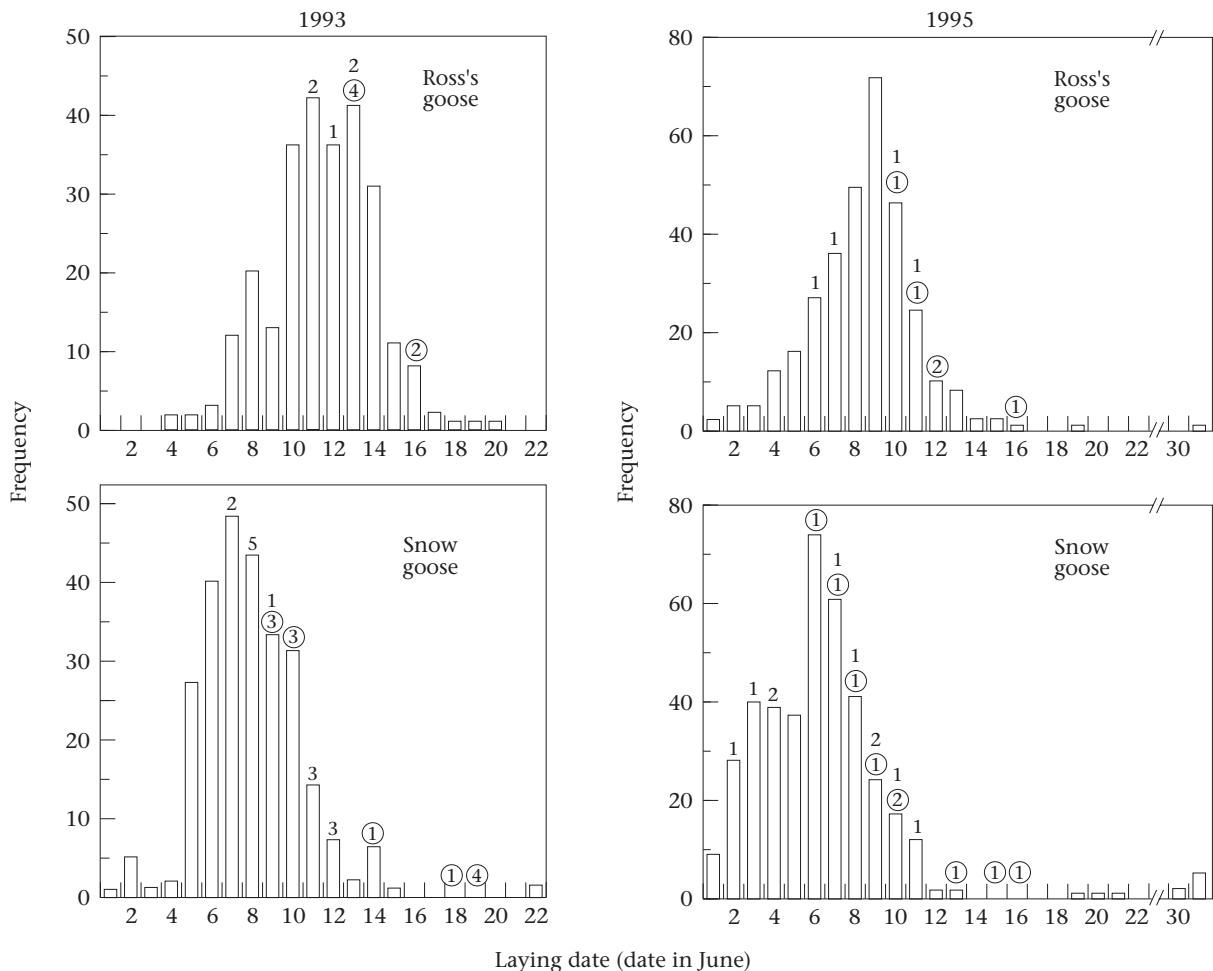


Figure 1. First egg dates (laying date) and copulations of lesser snow and Ross's geese, Karrak Lake, Nunavut, Canada, 1993 and 1995. Extrapair copulations are indicated by numbers in circles above each bar, and within-pair copulations are numbers above the bars without circles.

All extrapair copulations involved females on land, and most attempts were made while the female was on her nest (76%, 16/21 for snow geese; 82%, 9/11 for Ross's

geese). In all cases, extrapair copulations appeared to be forced, as females made loud vocalizations and appeared to resist. We saw no precopulatory displays prior to

Table 2. Within-pair (WPC) and extrapair (EPC) copulation attempts of Ross's and snow geese, Karrak Lake, Nunavut, Canada, 1993 and 1995

Year/stage	Ross's geese				Snow geese					
	Observation time (h)	WPC	EPC	WPC/h	EPC/h	Observation time (h)	WPC	EPC	WPC/h	EPC/h
1993										
Prelaying	12.0	2	0	0.17	0.00	14.7	2	0	0.14	0.00
Laying	28.2	3	6	0.11	0.21	42.5	12	6	0.28	0.14
Early incubation	72.1	0	0	0.00	0.00	27.6	0	6	0.00	0.22
Total	112.3	5	6	0.04	0.05	84.8	14	12	0.17	0.14
1995										
Prelaying		2	0				4	0		
Laying		2	2				6	6		
Early incubation		0	3				0	3		
Total		4	5				10	9		

Rates were calculated only for 1993; observations were made ad libitum in 1995.

extrapair copulation attempts, whereas within-pair copulations always were preceded by displays by both the male and female. When females were on their nests, they resisted extrapair copulation attempts by stretching their wings and neck out, making it more difficult for the male to grasp their neck and mount. When females were off their nests, they always tried to move away from the male by running or flying. The pair bond mate always returned and attacked the male attempting an extrapair copulation. All extrapair males were neighbours based on their subsequent movements to their own mate and territory. Although resisted by the female in all cases, at least half of extrapair copulation attempts appeared to be successful based on cloacal contact (snow geese: 58%, 7/12; Ross's geese: 50%, 3/6; 1993 data; Table 2). Among all successful copulations, 33% (7/21) were extrapair in snow geese and 38% (3/8) were extrapair in Ross's geese (1993 data). Thus observations of both attempted (47–55%, $N=65$) and successful (33–38%, $N=29$) copulations indicate that extrapair matings were relatively common in these geese.

In both species, within-pair copulations were seen only during the prelaying and laying periods, and they always occurred on water, either small ponds or meltwater puddles on the territory. In contrast, extrapair copulations were seen only during the laying period for Ross's geese (test of independence for reproductive period and type of copulation: $\chi^2_1=7.6$, $P=0.02$), and during the laying and early incubation periods for snow geese ($\chi^2_1=15$, $P=0.0006$; data combined for both years; Table 2). These reproductive periods were calculated for a large sample of the population and not for the particular pairs seen copulating; thus, reproductive periods are only general indications of the timing of copulations relative to the fertile period of females. For example, extrapair copulations during 'early incubation' may have involved some fertile females, as the last extrapair copulations were seen before the last known female in the population started laying (Fig. 1). Most extrapair copulations occurred during the laying period for both species (Fig. 1). On average, within-pair copulations occurred 3 and 4 days earlier than extrapair copulations for Ross's and snow geese,

respectively (three-way ANOVA of copulation date: effect of copulation type: $F_{1,61}=25$, $P<0.001$). Copulations were earlier in 1993 than 1995 (effect of year: $F_{1,61}=15$, $P<0.001$), and snow geese tended to copulate earlier than Ross's geese (effect of species: $F_{1,61}=3.7$, $P=0.059$; P for all interactions >0.42 ; Fig. 1).

When all reproductive stages were combined, extrapair copulations occurred 2.8 times more often in snow than in Ross's geese (1993 data; Table 2). Extrapair copulations were observed only during laying (0.21 copulations/h) for Ross's geese and during laying (0.14 copulations/h) and early incubation (0.22 copulations/h) for snow geese (Table 2). During laying and early incubation, extrapair copulation rates were greater for snow than for Ross's geese (logistic regression: effect of species: $\chi^2_1=8.0$, $P=0.005$); however the pattern of extrapair copulations differed between species (effect of date: $\chi^2_1=5.4$, $P=0.02$; interaction of species and date: $\chi^2_1=10.4$, $P=0.001$; 1993 data). Extrapair copulations in Ross's geese tended to occur in the middle of laying (1993 data, Fig. 1), while extrapair copulations in snow geese occurred in the middle of laying and after most birds had finished laying (Fig. 1). Within-pair copulations were observed only during prelaying and laying for both species (Table 2). Snow geese engaged in within-pair copulations 4.25 (0.17/0.04) times more often than did Ross's geese (Table 2); however, this difference was not significant in an analysis of the probability of observing a within-pair copulation using a logistic regression model that included species ($\chi^2_1=0.25$, $P=0.39$; $N=1183$ observation periods in 1993), date ($\chi^2_1=13.5$, $P=0.0002$) and the species by date interaction ($\chi^2_1=0.96$, $P=0.33$) as explanatory variables.

DNA Fingerprinting

Among 80 snow goose young sampled, we concluded that four young (5%) in three families (13%, 3/23) were the result of extrapair fertilization and one young (1.3%) in a fourth family (4.3%, 1/23) was the result of intraspecific brood parasitism (egg dumping). Overall, 74 young had no novel fragments and six had at least one (Fig. 2;

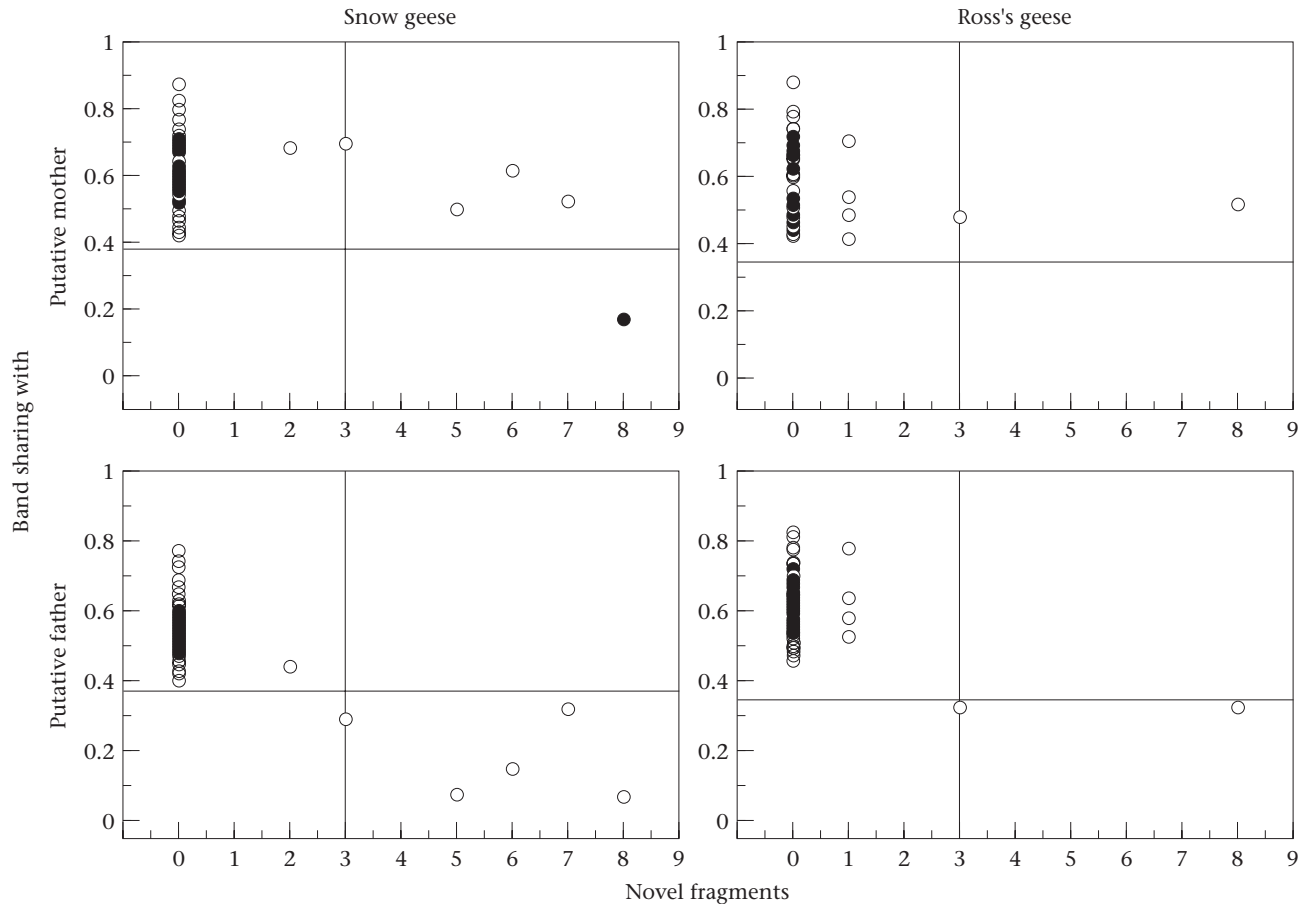


Figure 2. Band sharing between offspring and their putative parents in relation to the total number of novel fragments for lesser snow geese (left) and Ross's geese (right). We considered young that had fewer than three novel fragments (vertical lines) with a set of putative parents and band sharing with each parent ≥ 0.388 for snow or ≥ 0.345 for Ross's geese (horizontal lines) to be the progeny of those parents. The snow goose young excluded as a result of egg dumping is indicated by the filled circle in the lower right of the upper left panel.

range 2–8). The 74 young with no novel fragments had high levels of band sharing with both the putative father (0.562 ± 0.094 ; range 0.419–0.769) and mother (0.627 ± 0.103 ; range 0.421–0.875), indicating that they were direct descendants. The lower 99% CI (one-tailed) for band sharing between these offspring and their mothers was 0.388. We used this value as a general cutoff for excluding paternity in snow geese because this distribution did not overlap with the distribution of band sharing among putatively unrelated adults (mated males and females: 0.212 ± 0.075 , range 0.057–0.345, $N=23$ pairs). One of the six young with novel fragments had two novel fragments, but relatively high levels of band sharing with both the putative father (0.439) and mother (0.688), suggesting that they were related and that the novel fragments arose by mutation (Fig. 2). The five remaining young had three or more novel fragments. Four young had low levels of band sharing with the putative father (0.206 ± 0.121 ; range 0.069–0.333) and high levels with the mother (0.585 ± 0.091 ; range 0.500–0.700), suggesting that they were the result of extrapair fertilizations. The remaining young had low band sharing with both the putative father (0.065) and mother (0.171), suggesting that it was the result of intraspecific brood parasitism (see Fig. 2).

For Ross's geese, we did not recover DNA from three putative fathers and thus our sample of complete families was reduced from 27 to 24 broods (94 to 83 young). Of these, we concluded that two young (2.4%, 2/83) in 8.3% of families (2/24) were the result of extrapair fertilization. We found no evidence of intraspecific brood parasitism among these young or the young in the three additional families in which we recovered DNA from the putative mother and the young (see below). Of the 83 young with both putative parents analysed, 76 had no novel fragments and seven had at least one (Fig. 2; range 1–8). The 76 young with no novel fragments had high levels of band sharing with both the putative father (0.585 ± 0.089 ; range 0.421–0.811) and mother (0.589 ± 0.105 ; range 0.424–0.878), indicating that they were direct descendants. The lower 99% CI (one-tailed) for band sharing between these young and their mothers was 0.345. As with snow geese, we used this value as a cutoff for excluding paternity because the distribution of band sharing among putatively unrelated individuals (mated males and females) did not overlap this distribution (mean \pm SD = 0.213 ± 0.076 ; range 0.043–0.333, $N=24$ pairs). Five young had one novel fragment, but relatively high levels of band sharing with both the putative father (0.585 ± 0.108 ; range 0.500–0.759) and mother

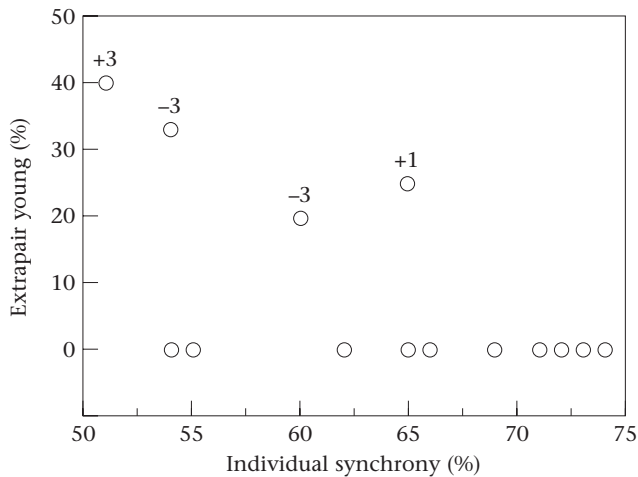


Figure 3. Extrapair young (%) in relation to individual synchrony (%) of nesting lesser snow geese, 1995. Individual synchrony is the percentage of other birds in the parentage sample that also were fertile during the fertile period of the focal female. Numbers by the four females with extrapair young indicate the number of days that they started laying before (negative) or after (positive) the mean laying date (7 June 1995). The one case of egg dumping was not included in the sample.

(0.573 ± 0.135 ; range 0.414–0.714), suggesting that they were related and that the novel fragments arose by mutation (Fig. 2). The remaining two young, with three and eight novel fragments, respectively, had low levels of band sharing with their putative fathers (0.273, 0.303) and high levels with the mother (0.519, 0.483), suggesting that they were the result of extrapair fertilizations (Fig. 2). For the three families in which we did not have a sample from the putative father, we concluded that all of the young were produced by the putative mother, as all mother–young band-sharing values were well above our cutoff of 0.345 (0.632 ± 0.086 , $N=11$, range 0.500–0.769). Thus, we found no evidence of dumped eggs in our sample of Ross's geese.

Relationship between Extrapair Copulations and Fertilizations

Although successful extrapair copulations were common in both species, they appeared to be relatively inefficient at fertilizing eggs. In snow geese, 33% (7/21) of all successful copulations were extrapair, yet extrapair fertilizations were uncommon (5% of young; $\chi^2_1=13.8$, $P=0.0002$). Similarly, in Ross' geese, 38% (3/8) of all successful copulations were extrapair, yet extrapair fertilizations were uncommon (2.4% of young; $\chi^2_1=17.3$, $P=0.0001$).

Effects of Breeding Synchrony and Nest Density

Extrapair paternity in snow geese was related inversely to breeding synchrony of individual females (Fig. 3; Spearman correlation: $\rho = -0.56$, $N=23$, $P=0.006$). Individual synchrony was the percentage of females in the

population that also were fertile when the focal female was fertile. Thus, extrapair young were more likely to occur when there were fewer fertile females in the population. Accordingly, extrapair paternity was more likely when females started nesting relatively early or late (Fig. 3). There was no similar relationship in Ross's geese ($\rho=0.16$, $N=24$, $P=0.45$), perhaps because just two nests had one extrapair young each. At the population level, synchrony of fertile periods was similar for the two species despite the trend towards more extrapair young in snow geese (synchrony index for the parentage samples: 66% for snow geese and 70% for Ross's geese).

Although the percentage of extrapair young was over two times greater in snow (5%) than Ross's (2.4%) geese, this difference was not statistically significant ($\chi^2_1=0.80$, $P=0.37$). The percentage of broods with extrapair young also did not differ between snow (13%) and Ross's (8.3%) geese ($\chi^2_1=0.27$, $P=0.60$). If the observed difference in the percentage of extrapair young were real, we would have needed a sample size of over 400 goslings from each species to detect a statistically significant difference.

Extrapair paternity was not related to nest density in either species. There was no significant correlation between the proportion of extrapair young in a nest and the number of conspecific nests within 20 m for either snow ($\rho = -0.06$, $P=0.78$, $N=23$) or Ross's ($\rho = -0.12$, $P=0.57$, $N=24$) geese. There also was no significant relationship between the proportion of extrapair young in a nest and first egg date for either snow ($\rho=0.0$, $P=1.0$, $N=23$) or Ross's geese ($\rho = -0.29$, $P=0.16$, $N=24$).

Paternity and Laying Order of Eggs

Among the four snow goose young that were sired by an extrapair male, three young were from the fourth or fifth egg (in clutches of five or six) and one was from the second egg in a clutch of three (maximum brood size in our sample was six young). When we examined the probability of extrapair paternity in relation to laying order, extrapair young tended to be from eggs laid later in the clutch (logistic regression, $\chi^2_1=3.0$, $P=0.08$). Clutch size was included in the logistic regression to control for clutch size differences among families. The single snow goose young from a dumped egg was the fourth in a clutch of five. Among Ross's geese, the two extrapair young were fourth in a clutch of four and fifth in a clutch of five.

DISCUSSION

Comparative analyses of birds have suggested that the level of extrapair paternity in a population is related to the frequency of extrapair copulations, the density of breeding individuals and the synchrony of their fertile periods (Birkhead & Møller 1992; Møller & Birkhead 1993; Stutchbury & Morton 1995; but see Dunn & Lifjeld 1994; Westneat & Sherman 1997). We detected low levels of extrapair paternity ($\leq 5\%$ of young) in snow and Ross's geese breeding in the high Arctic. Relative to other birds, these low levels of extrapair paternity provide an important exception to the comparative results. Snow and Ross's

geese might be expected to have higher levels of extrapair paternity as a consequence of their high frequency of extrapair copulation (>46% of all copulations), high nesting density and short synchronous breeding season. All extrapair copulations that we observed appeared to be forced, which suggests that forced copulations are not as successful a male reproductive tactic as might be expected. On the other hand, we found that extrapair paternity in snow geese was more likely to occur when relatively few females were fertile. This occurred when individual females nested asynchronously, either early or late in the season, and, to our knowledge, it is one of a few reported examples of a negative relationship between extrapair paternity and breeding synchrony. Most studies have reported a positive relationship or none at all (reviewed by Stutchbury & Neudorf 1998).

Forced Extrapair Copulations and Paternity

Relatively few studies have examined extrapair paternity in species with forced extrapair copulations, even though these species were among the first to interest researchers in alternative mating strategies of birds (e.g. Mineau & Cooke 1979; McKinney et al. 1984; Afton 1985). Consequently, little is known about the fertilization success of forced extrapair copulations. Previous studies of lesser snow geese (Quinn et al. 1987) and mallards, *Anas platyrhynchos* (Evarts & Williams 1987) documented that multiple paternity occurs in species with forced copulations. However, these studies primarily were demonstrating a new genetic technique and were not based on random samples from the population (Quinn et al. 1987), or used allozymes (Evarts & Williams 1987), which do not provide precise estimates of extrapair fertilization. Nevertheless, in both mallards (3–4% of young; Evarts & Williams 1987) and snow geese (2% of young; Lank et al. 1989a), previous estimates of extrapair fertilizations also were low. Our observations indicate that, although some forced extrapair copulations are successful (>33%), the tactic is relatively inefficient because of the low frequency of extrapair fertilizations ($\leq 5\%$ of young; see also Cooke et al. 1995, pp. 89–90).

This conclusion assumes that our observations of forced copulations were unbiased. There are two reasons to support this assumption. First, in 1993 we made focal observations of individual pairs, and such sampling is unlikely to be biased by the type of copulation. Second, focal sampling produced similar estimates of the rate of within- and extrapair copulations (i.e. unforced and forced) in both species (Table 2), suggesting that the type of copulation had no effect on probability of detection.

One possible explanation for the large difference between the frequency of extrapair copulations and their success is that within- and extrapair copulations may differ in their probabilities of successful insemination or fertilization. Although some forced extrapair copulations appear successful based on observation of apparent cloacal contact, successful insemination may be less likely or less sperm may be transferred when a female is resisting or attempting to escape. Success of extrapair copulations also may be reduced by within-pair copulations that

occur soon after extrapair copulation and thus dilute sperm from the extrapair male. In some species these 'retaliatory' copulations appear to be forced on the female by her mate (e.g. McKinney et al. 1984; Sorenson 1994). We did not see any within-pair copulations (forced or unforced) immediately after extrapair copulations, but they could have occurred later because females were not monitored very long after extrapair copulations, given our relatively short sample periods (10 min).

Lastly, forced extrapair copulations may result in relatively fewer fertilizations simply because they are directed primarily towards incubating, and thus nonfertile, females. Previous studies of forced extrapair copulations in snow geese found that 70–90% of extrapair copulations occurred after incubation had started (Mineau & Cooke 1979; Lank et al. 1989a). Mineau & Cooke (1979) and Lank et al. (1989a) suggested that males mate-guard when their mates are fertile, but afterwards attempt to force extrapair copulations with females that are not guarded as well, regardless of their fertile status. Consistent with these observations, we found that: (1) within-pair copulations occurred significantly earlier (3–4 days on average) than did extrapair copulations; and (2) extrapair paternity was associated with asynchronous nests, which tend to be produced later in the season when most females are no longer fertile and when males may have more time to pursue extrapair copulations. However, we also found extrapair young in two asynchronous nests from early in the season (see Fig. 3), which suggests that some males may be pursuing extrapair copulations when their own mates are fertile. Thus, the male tactic of mate guarding followed by pursuit of extrapair copulation may not be as consistent as believed previously. In white-cheeked pintails, *Anas bahamensis*, in the Bahamas, Sorenson (1994) also found a high frequency of forced extrapair copulations (28% of all successful copulations were forced extrapair copulations). However, in this species, forced extrapair copulations were directed primarily at fertile females, and males pursued extrapair copulations when their own mates were fertile, rather than afterwards (see also Afton 1985). Sorenson (1994) suggested that males may not pursue extrapair copulations after their mate's fertile period because they are in poor condition after a long period of defending a territory and guarding their mate.

Forced extrapair copulations are common in waterfowl (39 species), and occur in a variety of other species (reviewed by McKinney & Evarts 1998). Within waterfowl, there is considerable variation among species in the occurrence of forced copulations. For example, although extrapair copulations occur in snow and Ross's geese, they apparently do not occur in Canada, *Branta canadensis*, and pink-footed geese, *Anser brachyrhynchus*. Several researchers have argued that this variation is related to territoriality (McKinney et al. 1984; Gauthier 1988; McKinney & Evarts 1998). Species in which males defend a large territory do not have many forced extrapair copulations, whereas those that defend only a small area around the nest (either as a pair or just the female), such as Ross's and snow geese, are more likely to have forced extrapair copulations.

Extrapair Paternity and Egg Dumping in Other Waterfowl

Lank et al. (1989a) estimated the frequency of extrapair fertilization (2.4% of 45 777 goslings) and egg dumping (5.6%) using genetic plumage markers in lesser snow geese at La Perouse Bay, Manitoba, 1000 km southeast of our study site. Our estimates for snow geese also were low: 5% extrapair young and 1.3% dumped eggs. The frequencies of extrapair young ($\chi^2_1=2.23$, $P=0.14$) and egg dumping ($\chi^2_1=2.88$, $P=0.09$) did not differ significantly between populations. In both our study and Lank et al.'s (1989a), goslings were sampled at the nest, and thus, brood mixing could not have biased estimates. In a Swedish population of barnacle geese, *Branta leucopsis*, young were sampled after they left the nest, and brood mixing appeared to be a significant cause of excluded young (17% of young were excluded; Larsson et al. 1995; see also Choudhury et al. 1993). Although our estimates of extrapair paternity and egg dumping were similar to those reported by Lank et al. (1989a), there may be annual and geographical differences between populations. For example, egg dumping is more common when there is greater snow cover and, thus, fewer available nest sites (Lank et al. 1989b).

Nesting Density and Extrapair Paternity

Our results are not consistent with the hypothesis that nest density affects levels of extrapair paternity in birds, either within our study populations or relative to other species. Extrapair paternity and nest density were not correlated within our sample. In addition, the overall level of extrapair paternity was very low, despite the fact that our samples were collected from the largest known colony of geese. Our results are consistent with comparative analyses that found no effect of density on levels of extrapair paternity in birds (Lank et al. 1989a; Westneat & Sherman 1997). The effect of nest density on extrapair paternity probably depends on the fitness benefits that females gain from extrapair fertilizations, as well as their ability to control the success of fertilizations (Dunn et al. 1994; Lifjeld et al. 1994). In geese, extrapair copulations appear to be resisted, which suggests that females do not gain from extrapair fertilizations.

Breeding Synchrony, Egg-laying Order and Extrapair Paternity

We found that extrapair paternity was more likely to occur in snow geese when individual females nested asynchronously relative to other females, that is, early or late in the season. This inverse relationship between extrapair paternity and breeding synchrony is consistent with early hypotheses that assumed that males guarded their mates until after laying and then pursued extrapair copulations with later-nesting (asynchronous) females (Birkhead & Møller 1992). However, as mentioned above, some males may pursue extrapair copulations early in the season when their own mates are fertile.

Compared with other species, snow (66% synchrony index) and Ross's (70%) geese are among the most synchronously breeding birds (mean of 21 passerine species = 32%, range 8–73%; data from Stutchbury & Morton 1995). Again, the low level of extrapair paternity is consistent with earlier hypotheses that assume a trade-off between mate guarding and pursuit of extrapair copulations. Results from other studies of extrapair paternity and breeding synchrony are mixed: some species show a negative relationship (this study), but most show either no relationship (Dunn et al. 1994; Kempenaers 1997; Weatherhead 1997), or a positive relationship (see Bjørnstad & Lifjeld 1997; Stutchbury & Neudorf 1998).

In snow geese, we also found that extrapair young tended to occur among the last eggs laid in a clutch. This pattern could occur if males are copulating with their mates less often or guarding them less well towards the end of laying. To our knowledge, only two other studies have examined paternity in relation to laying order. Riley et al. (1995) found that the last-laid egg was more likely to be sired by an extrapair male in house martins, *Delichon urbica*, while Westneat et al. (1995) found no relationship between paternity and laying order in red-winged blackbirds, *Agelaius phoeniceus*.

In conclusion, our results generally support behavioural observations that male snow geese guard their mates when they are fertile and at other times attempt forced extrapair copulations with females that are not guarded well. However, a few early nests also contained extrapair young, which suggests that some males may pursue extrapair copulations when their own mates are fertile. Overall, there was a negative relationship between extrapair paternity and breeding synchrony, as relatively early or late nesting (asynchronous) females were the primary recipients of extrapair fertilizations. We did not detect a similar relationship in Ross's geese, perhaps because of the low number of extrapair fertilizations recorded. One of the most important results of our study is that relatively frequent extrapair copulations in both species of geese did not result in many extrapair fertilizations. Consequently, we argue that forced extrapair copulations are inefficient as an alternative reproductive tactic for males. Behavioural evidence (Mineau & Cooke 1979; this study) suggests that the tactic is inefficient largely because a high proportion of males attempt extrapair copulations with incubating females that are no longer fertile. Nevertheless, forced copulations are successful occasionally and may provide some males with significant increases in reproductive success.

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