# Intraspecific nest parasitism and extra-pair copulation in lesser snow geese

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**Abstract.** Intraspecific nest parasitism and extra-pair fertilization contributed significantly to individual reproductive success in a colony of plumage polymorphic lesser snow geese, *Chen caerulescens caerulescens*, studied for 14 years in northern Manitoba, Canada. Parasitic females preferred to lay in or adjacent to occupied, defended nests, rather than undefended nests. Nesting females usually rolled eggs that had been laid nearby into their nests. Nest-attendant males typically attacked the intruding female's mate, who usually remained at a short distance, thereby drawing the resident male away from the nest. Plumage genetics were used to estimate rates of both nest parasitism and extra-pair fertilization. Nests of homozygous dominant blue morph pairs produced 4·03% homozygous recessive white goslings ($N=4938$), which must have been unrelated to both parents, providing information on the rate of nest parasitism. Nests of homozygous recessive white morph pairs produced 2·12% blue goslings ($N=45\,777$), which must have been unrelated to either one or both parents, providing information on the rate of nest parasitism plus extra-pair fertilization. Using colony-wide estimates of the colour ratio of goslings produced (28·5% blue) and of the blue allele frequency in males (21%), it was calculated that nest parasitism accounted for 5·6% of hatching goslings, and that 2·4% of goslings were fathered by extra-pair fertilization.

Intraspecific nest parasitism and extra-pair copulation, and behaviour to prevent such activities, have been documented in numerous species of pair-bonded, pair-nesting birds (Yom-Tov 1980; Ford 1983; Mock 1983; Andersson 1984; McKinney et al. 1984). The outcomes of these conflicts of reproductive interest are less well documented, despite their important evolutionary consequences, as it is difficult to distinguish young produced by either process from each other or from that of the nesting pair (Gowaty 1985; Westneat 1987a). Successful intraspecific nest parasitism or extra-pair copulation results in parental care or resources being provided to non-kin. In general, natural selection will penalize traits favouring the production of unrelated conspecifics. Quantifying the effectiveness of these parasitic reproductive tactics is essential for evaluating evolutionary interpretations of behaviour that appears to promote or guard against this possibility (e.g. Trivers 1972; Barash 1976, 1977; Zeone et al. 1979; Power et al. 1981; Lanier 1982; Gowaty 1985; Møller 1987a, b;

Westneat 1987a).

Increased levels of intraspecific nest parasitism and extra-pair copulation have been suggested as intrinsic concomitants of colonial or social living (Hamilton & Orians 1965; Alexander 1975; Hoogland & Sherman 1976; Birkhead 1978; Gladstone 1979; Brown 1984; Emlen & Wrege 1986; Møller 1987b, c). Both activities are relatively frequent or conspicuous in many waterfowl, but rare in most geese (Weller 1959; Yom-Tov 1980; McKinney et al. 1983; Andersson 1984; McKinney et al.1984). We present information on a colonially nesting species of waterfowl, the lesser snow goose, *Chen caerulescens caerulescens*, studied at La Pérouse Bay, in northern Manitoba. Both intraspecific nest parasitism and extra-pair copulation occur at the colony (Cooke & Mirsky 1972; Finney 1975; Mineau 1978; Mineau & Cooke 1979a, b; Quinn et al. 1987). This paper describes how nest parasitism occurs, adds to previously published observations of extra-pair copulation, and uses a genetic marker to measure the proportion of hatching goslings attributable to each activity.

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## DETECTING PARENTAL EXCLUSIONS

Lesser snow geese have a genetically based plumage

**Table I.** Genotypes and expected phenotypic colour ratios of goslings derived from pair copulations, extra-pair copulations and intraspecific nest parasitism, for pairs of white (homozygous recessive, bb) and dark blue (homozygous dominant, BB) lesser snow geese

| Source of goslings | Possible gosling genotypes | Expected proportion of goslings | |
|---|---|---|---|
| | | Blue | White |
| White × white pairs (bb × bb) | | | |
| Pair copulation | bb | 0·00 | 1·00 |
| Extra-pair copulation | Bb, bb | 0·21 | 0·79 |
| Intraspecific nest parasitism | BB, Bb, bb | 0·29 | 0·71 |
| Dark blue × dark blue pairs (BB × BB) | | | |
| Pair copulation | BB | 1·00 | 0·00 |
| Extra-pair copulation | BB, Bb | 1·00 | 0·00 |
| Intraspecific nest parasitism | BB, Bb, bb | 0·29 | 0·71 |

The expected gosling morph proportions for extra-pair copulation by white females are the estimated B and b allele frequencies among the population of males at La Pérouse Bay. The expected proportion for intraspecific nest parasitism is the colour ratio of all goslings produced at the colony. See Methods for the derivation of these proportions.

dimorphism, and both white and blue colour phases breed at La Pérouse Bay. The plumage dimorphism of adults is determined by a single Mendelian locus. The blue allele (B) is incompletely dominant to white (b) with respect to the extent of dark feathers on the bellies of adults (Cooke & Cooch 1968; Cooke & Mirsky 1972; Rattray & Cooke 1984). This allows us to distinguish probable homozygote dominants (BB) from heterozygotes (Bb). Goslings are also dimorphic, but can be distinguished only as blue (BB or Bb) or white (bb).

Barring spontaneous mutation, plumage colour identifies certain goslings of homozygous pair types that are not related to one or both nest attendants: blue goslings in nests of two recessive white birds (W × W nests), or white goslings in nests of two homozygous dominant blue birds (B × B nests). Not all unrelated goslings can be detected by colour, but total parental exclusion rates can be calculated, under certain assumptions about intraspecific nest parasitism and extra-pair fertilizations as the source of the mismatched goslings, and about the colour morphs of the geese involved (Cooke & Mirsky 1972). Homozygous dominant BB females must produce blue goslings, regardless of the allele contributed by the male. Thus, white goslings hatching in B × B nests are due to nest parasitism only, and total parental exclusion rates

extrapolated from mismatched goslings in these nests are attributable to nest parasitism alone. Homozygous recessive bb (white) females can produce white or blue goslings, depending on whether a B or b allele is contributed by the male gamete at fertilization. Thus, blue goslings hatching in W × W nests can result from either nest parasitism or extra-pair copulation, and total parental exclusion rates extrapolated from mismatched goslings in these nests include goslings produced by both activities. Possible genotypes of offspring from pair copulation, extra-pair copulation, and intraspecific nest parasitism, in B × B and W × W nests, are shown in Table I. Using certain testable assumptions, we can solve for the rate of extra-pair fertilization alone by combining information from B × B and W × W nests.

## METHODS

The La Pérouse Bay snow goose colony, located near the southern edge of the species' arctic breeding range, 40 km east of Churchill, Manitoba, has been studied since 1968. Both white- and blue-phase morphs breed in the colony, with white birds predominating (ca. 73·4% of females and 71·5% of males), and there is strong positive assortative

mating by colour morph (Cooch & Beardmore 1959; Cooke et al. 1976). General field methods are described by Finney & Cooke (1978), Rockwell et al. (1983) and Cooke et al. (1985). Each year several thousand nests were visited during hatching, and the plumage phenotypes of nest attendants and hatching goslings were recorded. We used this large database to estimate rates of successful intraspecific nest parasitism and extra-pair fertilization.

We directly observed attempts at intraspecific nest parasitism and extra-pair copulation in 1976 and 1977, from a live-in blind built in an otherwise undisturbed part of the colony, thereby minimizing disruption of the nesting birds (Mineau 1978). Sampling techniques were described by Mineau & Cooke (1979a). Complete information on the behaviour of intruders and nest attendants was not always known or recorded. We used all available information for each aspect of behaviour or morph type that we report.

In 1977, we tested the reaction of geese to foreign eggs. Eggs from abandoned nests were placed either at the edge of the nest cup or 1 m from the nest, and an outcome was determined 24 h later. Experimental eggs were either added to the clutch (presumably rolled in by the nesting female, Prevett & Prevett 1972), or remained outside the nest, or disappeared, presumably due to depredation. Tests were conducted prior to or up to 9 days after the start of incubation.

### Calculating Rates of Parental Exclusions

We estimated the total number of goslings attributed to nest parasitism or extra-pair fertilization by using the following exclusion equation

$$N_{ob} = (D_I \times N_I) + (D_E \times N_E)$$

where $N_{ob}$ = number of observed parental exclusions, $D_I$ = the probability of detecting exclusions due to intraspecific nest parasitism, $N_I$ = the total number of goslings due to intraspecific parasitism, $D_E$ = the probability of observing exclusions resulting from extra-pair fertilization, and $N_E$ = the total number of goslings resulting from extra-pair fertilization. Total rates of intraspecific nest parasitism and extra-pair fertilization were calculated by dividing $N_I$ or $N_E$, calculated from the above equation, by the total number of goslings in the sample.

Observed exclusions ($N_{ob}$) consisted of blue goslings hatching in W × W nests and white goslings hatching in B × b nests. W × W nests were those with two white attendants. B × B nests, with pairs of presumed homozygous dominants, were defined by the plumage scores of nest attendants. Adult blue-phase geese were assigned a score from 2 to 6, based on the extent of breast coloration (Cooke & Cooch 1968). Birds scored as 5 or 6, and paired to any blue goose, are nearly all homozygotes (Rattray & Cooke 1984). To minimize contamination from white goslings produced by the nesting female, only pairs consisting of a bird scored as 6 with a mate scored as either 5 or 6 were used in the sample of B × B nests. These pairs did not differ in the proportion of white offspring hatching in their nests (6 × 6: 2580 blue:106 white; 6 × 5: 2181 blue:94 white; $G = 0.11$, $P = 0.74$). If the female of such pairs was the only heterozygote, she could produce a white gosling through extra-pair copulation. Such an event would cause an overestimate of nest parasitism rate and an underestimate of extra-pair fertilization rate in our population. Nests with three or more excluded goslings and no matching goslings were excluded from our sample (21 of 11 884 W × W nests, 8 of 1295 B × B nests). The colour of attendants at these nests may have been misassigned or misrecorded in the field, or the exclusions may have occurred due to nest takeovers or processes other than intraspecific nest parasitism or extra-pair copulation. Using these nests would increase the estimated rates of both parasitism and extra-pair fertilization, but would not alter the relative importance of the two events.

As explained above, due to plumage genetics the detection probability for extra-pair copulation, $D_E$, is zero for homozygous blue females. For B × B nests, the exclusion equation thus reduces to a calculation of the number of goslings due to intraspecific nest parasitism only. Quasi-parasitism (Gowaty 1985; Emlen & Wrege 1986), in which a nesting male fertilizes a non-attendant female, who then lays in the pair's nest, would be included as nest-parasitism in our calculations.

The detection probabilities, $D_I$ and $D_E$, that were used to calculate the numbers of excluded goslings assumed that parasitism and extra-pair copulation were random with respect to the plumage phenotypes of nest parasites, nest attendants and geese engaging in extra-pair copulation. The proportion of white goslings produced on the colony during the study period, 0.715 ($N = 71\,274$), was used as the probability of detecting white goslings in B × B nests; the proportion of blue goslings, 0.285, was used as the probability of detecting blue goslings
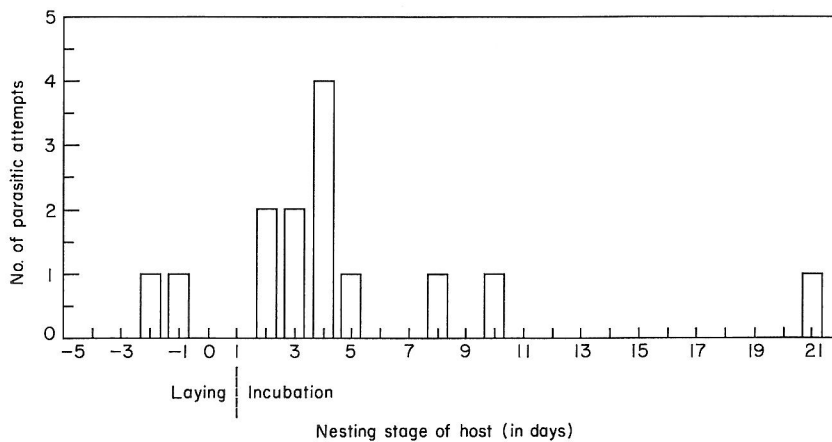
**Figure 1.** The temporal distribution of parasitism attempts relative to incubation date by the nesting female.

resulting from nest parasitism in W × W nests. The expected values are the colour ratio of the progeny of all nesting geese, not only the W × W and B × B pairs. We used an estimate of the proportion of B alleles in males, 0·21, as the expected proportion of blue goslings produced by extra-pair fertilization in W × W nests. This value is an empirical estimate based on the frequencies of specific plumage pair types, using the 2–6 scale for blue geese mentioned above and estimates of heterozygosity for each plumage and pair type (Rattray & Cooke 1984), and checked against the actual gosling colour ratio produced by each specific pair type (1973–1985).

We tested assumptions of randomness with respect to the plumage of participants in intraspecific nest parasitism and extra-pair copulation against data gathered during behavioural observations. We tested the colour ratios of two samples of goslings of probable parasitic origin against the expected colour ratio of progeny from parasites. Egg-laying sequences of nests visited daily during laying were used to detect parasitic eggs ($N = 2997$ nests, from 1975 to 1982). When two eggs were laid on the same day, goslings hatching from these eggs provided a sample in which half were of parasitic origin, assuming equal hatchability of attendant and parasitic eggs laid at the same stage of the nesting cycle. A second sample of eggs was obtained from unhatched eggs with partially developed embryos. As most of these were laid by parasites after the attendant began incubation, these embryos provided additional information on the colour ratio of probable parasitic eggs. Data were available from 1980 to 1986.

We tested our estimated extra-pair copulation and intraspecific nest parasitism rates by comparing the predicted and observed pattern of blue goslings in W × W nests by clutch size. To obtain predicted values, we tallied egg sequence irregularities that might reflect intraspecific nest parasitism: multiple eggs per day, eggs found outside the nest, eggs laid after none had been laid for 2 days, eggs laid 2 or more days after the onset of incubation, and eggs noted in fieldbooks as parasitic ($N = 1978$ nests, 1975–1982). This provided a relative index of parasitism among clutch sizes that was independent of the estimate derived from colour ratio.

We pooled data from 14 years to obtain robust, long-term estimates of levels of intraspecific nest parasitism and extra-pair fertilization. The amount of nest parasitism in lesser snow geese varies substantially among years (Finney 1975; Syroechkovskiy 1979), but annual sample sizes were too small to provide accurate yearly estimates of extra-pair fertilization rates. However, the results reported here are not artefacts created by pooling data over years.

## RESULTS

### Observations of Parasitic Females

Strange female snow geese frequently approached nests during and after laying by the attendant pair. Of approaches made to nests where the onset of incubation was known, only 43% occurred prior to 4 days into incubation ($N = 14$, Fig. 1). After this time, added eggs have little

**Table II.** Results of egg-rolling experiments

| Distance egg was placed from nest | Total clutch size | Outcome | | |
|---|---|---|---|---|
| | | Egg was added to clutch | Egg remained outside nest | Egg disappeared |
| Edge of cup | 2–5 | 13 | 1 | 0 |
| 1 m | 2–3 | 5 | 0 | 1 |
| 1 m | 4–5 | 7 | 6 | 2 |
| 1 m | 6–7 | 4 | 0 | 1 |

chance of hatching with the attendant's clutch (Davies & Cooke 1983). Snow goose nests are not closely attended during the laying period, and parasitic females might lay eggs in unattended nests relatively easily. However, all six cases of parasitic laying were observed at attended, defended nests. Intruding females were usually accompanied by mates (93%, $N=27$). Typically, the pair approached a nest site, and both attendants defended the site. Males prevented females from reaching nests only when the pair's approach was aerial ($N=4$) rather than on the ground ($N=8$). Most often, the intruding male remained a short distance away from the actual nest hummock (85%, $N=13$), the attendant male moved away from the nest to attack him, and the intruding female approached the nest site. The attendant female usually remained sitting on the nest. Intruding females approached the sitting bird, and in some cases displaced it by pushing with their breasts. Parasitic females spent 1, 4, 5, 10 and 28 min sitting on or next to the nest prior to laying. When not shielding their heads to ward off blows from the attendant pair, parasites often engaged in nest-building activities. Five cases where the intruder left a nest site without laying were followed by another parasitism attempt; in 19 cases the intruders' subsequent behaviour was unknown.

Observations of intraspecific nest parasitism may have been biased towards conspicuous encounters at occupied sites. A continuous record of nest-searching behaviour was obtained through observation of a lone female for 4·8 h early in the season. The bird approached at least 15 unoccupied and 18 occupied sites. She was chased away from all occupied sites by both members of the pair. This female remained at a nest cup at one unoccupied site for 34 min, pulling at nest material, but she did not lay. From this lone female's failure to lay at the unoccupied sites she visited, the lack of other

observations of laying at unoccupied sites, and the six cases where laying was observed, we conclude that parasites preferred to try to lay at occupied sites.

Four of the females approaching nests could be aged from coloured leg bands. Two had been banded as goslings 2 years earlier, and would have been breeding for the first time when seen. Two other females had been banded as adults. If parasites constituted a random age sample of the banded breeding population, we would have been unlikely to have seen two young out of four parasites, since 2-year-olds made up only 12·1% of the banded breeding females encountered at the colony during the years of observations ($N=494$, binomial test for two of four versus 0·121, $P=0·07$). One 2-year-old and one adult parasite were individually identified from their bands, and both birds incubated nests in subsequent years, showing that individuals shifted their breeding tactic from year to year.

Parasitic females need not lay inside the nest to obtain incubation for eggs. In three of the six observations of parasitic laying, the egg was laid outside the nest and was subsequently rolled into the nest by the resident female. In experiments testing the reaction of the geese to foreign eggs (see Methods), eggs placed at the edge of the nest cup were nearly always rolled into the nest (Table II). Most of the eggs placed 1 m away were also brought in, but females with clutches of four or five left the egg out of the nest more often than did those with larger or smaller clutches (Table II, $G=7·84$, $df=2$, $P=0·02$). Stage of incubation had no effect on female response, as also found by Prevett & Prevett (1972). One female that left the experimental egg outside the nest had earlier left out an egg laid naturally near her nest during her laying period. Four eggs placed 1 m from the nest disappeared, presumably due to predation. All four

were from the 10 tests conducted prior to the start of incubation, while no eggs disappeared in the 16 later trials ($G = 8.86$, $df = 1$, $P = 0.003$). These results suggest that the risk of loss for parasitic eggs laid near nests is lower once incubation has begun.

### Observations of Extra-pair Copulation

Extra-pair copulation, previously described by Mineau & Cooke (1979a), usually involved breeding males who attempted forced matings at the nests of neighbouring breeding females. In four cases, however, a breeding male attempted forced copulation with a female that intruded on a pair's territory. Most attempts were made after the male's mate or the attacked female had begun incubation (37 out of 41 and 38 out of 54, respectively). Both observations suggest that males mate-guard females more closely when they are fertile, and subsquently attempt extra-pair copulation with less well-guarded birds, regardless of their fertilizability (Mineau & Cooke 1979a). No determination of the reproductive success of extra-pair copulation was possible from behavioural observations.

### Parental Exclusion Rates

From 1973 to 1986, B × B nests contained 199 white goslings out of a total of 4938. Using the equation and logic presented in the Methods, and the parental exclusion detection probability for parasitism in B × B nests given in Table I, we calculated a parasitism rate of 5.64% of all goslings ($N_1 = (199/0.715) = 278.3$; parasitism rate $= 278.3/4938$). During these same years, W × W nests contained 969 blue goslings out of 45 777 total. Using the full exclusion equation, the parasitism rate calculated for B × B nests, and the exclusion detection probability for extra-pair fertilization in W × W nests given in Table I, we calculated an extra-pair copulation rate of 2.42% ($N_E = ((969 - (0.285 \times 0.0564 \times 45\,777))/0.21 = 1110.5$, extra-pair fertilization rate $= 1110.5/45\,777$). These rates suggest that 70% ($5.64/5.64 + 2.42$) of blue goslings in W × W nests occur because of nest parasitism, and 30% are due to extra-pair copulation.

The accuracy of the preceding calculations, and their applicability to other pair types of nesting snow geese at the colony, depend on two assumptions: (1) parasitic progeny are a representative colour sample of all goslings produced in the breeding colony, in both W × W and B × B nests,

and (2) extra-pair fertilizations occur without regard for male or female colour, at least for W × W pairs. These assumptions are tested below.

Females of both colour morphs were observed attempting parasitic laying. Fourteen were white, 10 were blue, and the colours of four were not recorded. The blue proportion among the birds where colour was recorded is not significantly different from that expected if the parasitic population were a random colour sample of female breeders in 1977 and 1978 (0.27 blue, $N = 3410$, binomial test: $N = 24$, $P = 0.17$). The colour ratio of attendant females was 18 white to seven blue, exactly as expected from the colour ratio of the birds in the observation area. There was no association between the colour of the intruding female and the attendant female approached (intruder colour × attendant colour: W × W, $N = 11$, W × B, $N = 4$; B × W, $N = 7$; B × B, $N = 3$; $G = 0.03$, $df = 1$, $P = 0.85$).

We also tested for colour bias in parasitic eggs in W × W nests. First, we examined the colour ratio of goslings in cases where two eggs were laid in a nest on the same day. If the hatchability of parental and parasite eggs laid at the same time is equal, we can assign half the young hatching from such eggs to the parents, and half to nest parasites. By restricting the sample to W × W nests, the parent's half will be white (ignoring, for the moment, extra-pair copulation), and the remaining goslings will be a colour sample of young produced from parasitic eggs. We identified 212 white and 32 blue goslings hatching from such eggs (1975–1986). Attributing half the sample to the attendants, which were all white, leaves a proportion of 0.29 blues among the putative parasitic goslings (32 of 122). This is virtually identical to the proportion of blue goslings produced on the colony during these years, 0.285 ($N = 42\,409$), and is consistent with no colour bias in parasitism.

Our second test involved the colour ratio of partially developed goslings from eggs that failed to hatch in W × W nests. Most of these resulted from parasitic eggs laid in nests after incubation had begun. Of those judged to be 3 days or more from hatch (1980–85), 17 out of 74 (0.23) were blue (binomial against 0.285, $P = 0.36$). This test is less strong than the previous one, since the slow developing white embryos of nest attendants would be included in the totals. Indeed, embryos a day or two from hatch reflected the nest attendant genotype more closely (0.11 blue, 4 of 38).

**Table III.** Probable origins of eggs producing blue goslings in W × W nests

| Laying sequence of egg producing blue gosling | No. of eggs |
|---|---|
| Probable nest parasitism: | |
|   One of two eggs laid per day | 23 |
|   Other egg from a nest in which two eggs were laid per day | 9 |
|   Egg laid after the start of incubation | 12 |
| Possible nest parasitism: | |
|   First egg, followed by a day or more before next egg was was laid | 3 |
| Total nest parasitism | 47 |
| Probable extra-pair fertilization: | |
|   Egg was laid in the middle of the normal laying sequence | 12 |
| Possible extra-pair fertilization: | |
|   First egg laid in normal sequence | 8 |
| Total extra-pair fertilization | 20 |

Among extra-pair copulations, we found no colour bias in the frequency of attempts or in morph combination of the participants. Of extra-pair copulation attempts by banded males nesting in the observation area, 28 were by white and 14 were by blue males, exactly the proportion expected from the frequency of each morph in the area. The sample of all males attempting extra-pair copulation was 0·30 blue ($N = 110$), compared with 0·29 (1977–1978, $N = 3255$) expected for the colony as a whole (binomial against 0·29, $P = 0·90$). Males showed no colour bias in their extra-pair copulation attempts on females. The proportion of blue females in the observation area was 0·29. The proportion of attempts that were made on blue females was 0·21 ($N = 109$), a biased but not statistically significant underrepresentation of blues ($G = 2·68$, $df = 1$, $P = 0·10$). We observed no association between the colour morph of a male attempting extra-pair copulation and that of the female (male colour × female colour: W × W, $N = 63$; W × B, $N = 19$, B × W, $N = 23$; B × B, $N = 4$; $G = 0·90$, $df = 1$, $P = 0·34$).

Examination of egg-laying sequences in W × W nests that hatched blue goslings provides another estimate of the proportion due to extra-pair copulation versus intraspecific nest parasitism (Table III). Eggs fertilized outside the pair bond should be laid in regular sequence, while parasitic eggs usually, but not necessarily, create sequence irregularities, such as two eggs laid per day or skips of several days between eggs. Of the eggs where the laying sequence was known, 30% in the W × W nests that hatched into blue goslings may be best

attributed to extra-pair fertilization. If first-laid eggs, whose source is the most problematical, are excluded, 21% of the goslings are best attributed to extra-pair fertilization. Neither of these figures is significantly different from 30% (binomial tests, NS). We conclude that one out of every 40–50 goslings was related to the attendant female, but not to the attendant male.

### Testing Variation by Clutch Size and Pair Type

Cooke & Mirsky (1972) found that the proportion of blue goslings in W × W nests increased with clutch size, and argued that this supported intraspecific nest parasitism as the source for blue goslings. Mineau & Cooke (1979a) speculated that extra-pair fertilization might account for a baseline level of mismatches across all clutch sizes, while an intraspecific nest parasitism component would account for the increase related to clutch size. We tested whether the global proportions of blue goslings in W × W nests that we attributed to nest parasitism and extra-pair fertilization were consistent with this hypothesis.

We generated two expected distributions of blue goslings by clutch size: one for goslings attributable to extra-pair fertilization, the other for goslings attributable to intraspecific nest parasitism. We calculated separate expected distributions using both 21% and 30% as the proportion of goslings arising through extra-pair fertilization. The distributions for extra-pair fertilization assumed that a gosling's probability of being derived by extra-pair fertilization was independent of clutch size, as
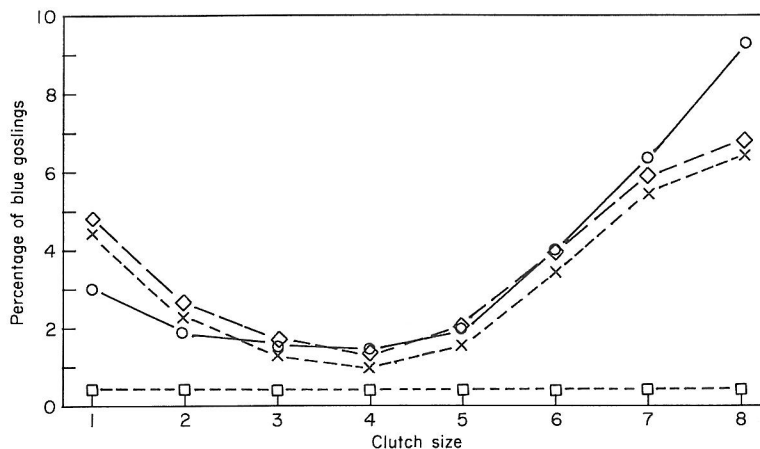
**Figure 2.** Observed (solid line) and expected (dashed lines) percentages of blue goslings hatching in W × W nests, as a function of clutch size. The expected proportions of goslings due to extra-pair copulation (□), intraspecific nest parasitism (X), and totals (◇) are indicated. See text for derivation of the expected lines. Total gosling samples for each clutch size (1–8+) are: 132, 1489, 7132, 17006, 11359, 3942, 1107 and 353, respectively.

stated in the hypothesis. Of the blue goslings hatching in W × W nests where clutch size at hatch was known (2·05% of 44318 goslings), 21% (or 30%) were attributed to extra-pair fertilization, producing an expected extra-pair fertilization baseline rate of 0·43% (or 0·62%) for all clutch sizes. A clutch-size specific index of intraspecific nest parasitism was determined from egg-laying sequence irregularities at different clutch sizes (see Methods). The proportions of presumed parasitic eggs at each clutch size were then uniformly scaled so that total nest parasitism would account for the 79% (or 70%) of blue goslings not attributed to extra-pair copulation. The observed frequency distribution was compared with a predicted one generated by multiplying parasitism rates by the total number of goslings hatched at each clutch size.

There was reasonable agreement between the observed and predicted proportions of blue goslings hatching from different clutch sizes, although the predicted proportions are systematically higher at smaller clutch sizes and lower at larger ones (Fig. 2, using 21% and 79%). A goodness-of-fit test showed no significant difference between observed and expected proportions ($\chi^2 = 10·8$, $df = 7$, $P = 0·15$). Similar results were obtained using 30% and 70% as expected proportions. Mineau & Cooke's (1979a) hypothesis is a workable explanation for the increased proportions of blue goslings with increasing clutch size, given the estimated parameter values. The pattern of parasitism rates,

lowest at intermediate clutch sizes, is consistent with the behavioural observations in the egg-rolling experiment (Table II).

A change in gosling colour ratio with clutch size due to parasitism should occur for all pair types of geese. The genetic expectation for goslings produced by pairs containing one or two blue birds are 50% (Bb × bb), 75% (Bb × Bb), or 100% (BB × bb, Bb, or BB) blue. Since the genetic expectation of blue goslings from nest parasitism by a random colour sample of parasitic pairs is lower (28·5%), the proportion of white goslings hatched by nesting pairs that include a blue goose should increase with clutch size. This occurred in mixed pairs (all blue × white), blue × blue pairs with one or more likely heterozygotes, and probable blue homozygote pairs (Table IV). These results provide evidence that nest parasitism occurs in all pair types of nesting geese.

### Testing a Model of Nest Parasitism Only

Our original calculations showed that total parental exclusion rates were higher in W × W than B × B nests, and we attributed this difference to the detectability of goslings produced through extra-pair copulation in W × W, but not in B × B nests. An alternative hypothesis is that parasitism rates are higher in W × W nests, and that extra-pair copulation is not a significant factor. This could occur if there were a blue bias among nest parasites,

Table IV. Percentage of blue goslings as a function of clutch size at hatch for different parental pair types

| Parental phenotypes | Clutch size at hatch* | | | | | | Significant groupings† |
|---|---|---|---|---|---|---|---|
| | 1–2 | 3 | 4 | 5 | 6 | 7+ | |
| W × W | 2·1 (932) | 1·6 (2543) | 1·5 (4543) | 1·9 (2844) | 3·9 (747) | 6·9 (254) | 1–5, 6, 7 |
| W × Blue | 57·0 (243) | 58·2 (706) | 60·2 (1201) | 58·1 (775) | 53·4 (169) | 53·8 (65) | 1–5, 3–7 |
| Blue × Blue | 89·3 (183) | 88·7 (493) | 88·3 (854) | 87·3 (518) | 83·9 (115) | 76·3 (35) | 1–5, 4–6, 7 |
| B × B | 93·9 (99) | 97·9 (284) | 97·5 (517) | 95·0 (308) | 91·7 (61) | 87·2 (18) | 1–5, 6–7 |

* Values are means of percentages of blue goslings at each nest. Numbers in parentheses are number of nests. Data for all pair types were significantly heterogeneous among clutch sizes (ANOVA, $P < 0.01$).
† The significant groupings of data under Student–Newman–Keuls multiple comparison tests are shown ($P < 0.05$). W × Blue includes all nests with white × blue attendants. Blue × Blue includes all blue × blue pairs except the homozygous B × B pairs, tabulated at the bottom.

or if W × W nests were more susceptible to successful parasitism. If we credit all of the exclusions observed in W × W nests to nest parasitism alone, we obtain a parasitism rate of 7·43% ($N_I = 969/0.285 = 3400$; nest parasitism rate $= 3400/45\,777$), 31% higher than in B × B nests (7·43 versus 5·64). Although examination of several separate data sets failed to show non-random colour ratios among putative parasites, their eggs, or their hosts, we also tested whether the observed data are consistent with this alternative hypothesis.

A 31% higher parasitism rate predicts that 0·35 of females attempting parasitism would be blue, rather than 0·27 (see above), which is not significantly different from the observed ratio of birds whose colour was recorded (see above, $N = 24$, $P = 0.63$). Direct observation thus failed to reject either the random or blue-biased null hypothesis. If blues parasitized by an extra 31%, then the proportion of blue parasitic goslings should have been 0·37 rather than 0·285, as expected under the random null hypothesis. Both the colour ratio of goslings hatching from multiple eggs per day (see above), and that of partially developed embryos (see above) have significantly lower ratios than predicted (binomial against 0·37: two eggs per day: $N = 122$, $P = 0.02$; embryos: $N = 74$, $P = 0.02$). These data suggest that there was no colour bias in nest parasitism.

Higher susceptibility of W × W nests to parasit-

ism is more difficult to test directly, as we observed only six cases of parasitic laying. Potential parasites approached nest sites of different morphs exactly as expected under the random null hypothesis. Blue and white females did not differ in their tendency to adopt eggs in our adoption experiments or in the adoption experiments of Prevett & Prevett (1972). Indirect evidence against a colour bias comes from the overall similarity in the reproductive performance of the two morphs at La Pérouse Bay, including egg hatchability and clutch size (Cooke et al. 1985; Rockwell et al. 1985). In addition, the distributions of nest initiation dates, which might affect the probability of parasitism, were nearly identical for the two morphs (ANCOVA for nest initiation date of phases, controlling for year, partial $F$ for colour-phase term $= 0.00$, $N = 2296$, NS). If white females were substantially more susceptible to nest parasitism, their mean clutch size should be higher than that of blue females, unless parasitized birds reduced their clutch size (Andersson & Eriksson 1982), or white females laid smaller clutches and parasitism balanced out the difference. We believe the former is extremely unlikely for arctic geese. If the latter were true, clutches of white females should differ more in size from those of blue females in years with higher parasitism rates, but this does not occur (Lank, Cooch, Rockwell & Cooke, unpublished data). We conclude that the discrepancy between exclusion

rates is not accounted for by higher nest parasitism by blue females or higher susceptibility to parasitism by white females.

## DISCUSSION

Nest parasitism and extra-pair copulation are significant components of the reproductive strategies of female and male lesser snow geese. We calculated that nest parasitism accounted for 5·6% of all goslings produced at La Pérouse Bay between 1973 and 1986, and that extra-pair fertilization accounted for 2·4%.

Although the alternative reproductive tactics of snow geese are effective, goose behaviour seems less well-developed than that of other species. Parasitic laying by females is only moderately well-timed with respect to attendant incubation. Females do not appear to discriminate their own eggs from parasitic eggs. Egg-tossing (rolling eggs out of the nest) is absent, and, instead, most females will adopt foreign eggs placed near their nests. While some species use subtle cues to recognize and approach fertilizable females (e.g. Jones 1986), extra-pair copulation in snow geese appears to be poorly timed relative to female fertilizability (Mineau & Cooke 1979a). We have not seen males copulating with their mates following extra-pair copulation of the mate, as has been reported in some species (cf. Barash 1977; McKinney et al. 1983). Constraints on goose behaviour are considered below.

### Behaviour of Nest Parasites

Nest parasitism is commonly considered an alternative reproductive strategy for females, but male snow geese also have a reproductive interest and play a role in parasitism attempts. Most females seen attempting intraspecific nest parasitism were accompanied by a mate, as in other waterfowl species (Weller 1959; Andersson & Eriksson 1982). Lone females were unsuccessful at gaining access to occupied sites. Males usually facilitated their female's access to the nest site by remaining at a distance from the hummock and drawing the attendant male away from the nest. Intruding males left their mate unguarded as she moved towards the nest site, and four forced copulation attempts by resident males on intruding females were observed. There is thus a paternity risk in being separated from the female, and remaining away from the nest site may be a specialized behavioural tactic that promotes the female's chance of laying. In any case, it served this function. Male snow geese of Wrangel Island, north of Siberia, also stood off to the side while parasitic females were at the nest (Syroechkovskiy 1979).

Cooch (1958), working in the high arctic, and Finney (1975), at La Pérouse Bay, described a different situation where nest parasitism occurred. Nesting areas were invaded by flocks of geese, consisting of both immature geese and breeders, which completely swamped nest defence. Finney (1975, page 21) reported that he 'often found one to four new eggs in several of the nests' in the wake of such invasions.

Limited observations suggest that the parasitic population was biased towards 2-year-old females (Finney 1975). On Wrangel Island, many parasitic eggs and eggs dumped in unincubated piles were longer and thinner than those laid by nest attendants (Syroechkovskiy 1979). Long eggs were attributed to first-time breeders, who would in that case comprise most parasitic geese.

The timing of parasitic laying relative to incubation of the clutch is critical to the hatching success of parasitic eggs. Eggs added to nests 2, 4, and 5 or more days into incubation have a 37%, 29% and 0% chance of hatching, respectively (Davies & Cooke 1983), and abandonment of late-laid eggs is the principal disadvantage of parasitic laying (Lank, Rockwell & Cooke, unpublished data). Parasites could avoid this reproductive loss by laying in undefended nests prior to host incubation. They preferred occupied sites, however, and most parasitic events occurred after incubation had begun (Fig. 1). Laying eggs at occupied sites minimizes the risk of laying in an abandoned nest or one that will fail prior to the onset of incubation (17–33% of nests per year, Cooke & Rockwell, unpublished data). Parasitic laying occurs later in the season than non-parasitic laying (Lank, Rockwell & Cooke, unpublished data), perhaps because parasitism is biased towards younger, later-breeding females, and unattended nests may be difficult to find.

The frequency of nest parasitism, and the probable effect on nest attendant fitness, are less at La Pérouse Bay than in the northern part of the species' range. Extremely large unincubated dump nests have been reported at northern snow goose colonies, especially during years with restricted nesting habitat (Cooch 1958; Syroechkovskiy 1979;

Prevett & MacInnes 1980; Bousfield & Syroech-kovskiy 1985). In certain years, parasitism also increased the clutch size of incubated nests far more than has been observed at La Pérouse Bay (e.g. changes from 3·7 to 5·9 eggs per nest at Wrangel Island; Syroechkovskiy 1979). There are no quantitative data on what proportion of active nests is swamped by such events.

## Behaviour of Nest Attendants

Attendant pairs were aggressive towards potential parasites, but they often failed to prevent the female from reaching the nest site. Cooch (1958, page 22) reported that on Southampton Island 'the sexes square off', with male fighting male and female fighting female. Confrontation within sexes is consistent with our observations, but most La Pérouse Bay females stayed on or near the nest. The nesting male's tendency to approach the intruding male, and the tendency of the female to remain at the nest, constrained their defence against intraspecific nest parasitism.

The most intriguing aspect of attendant behaviour was the tendency of females to adopt parasitic eggs by rolling them into nests (Prevett & Prevett 1972). The literature on intraspecific and interspecific avian nest parasitism describes subtle strategies of egg tossing or removal of parasitic eggs (e.g. Weller 1959; Emlen & Wrege 1986). Active adoption is unusual among birds (Prevett & Prevett 1972; cf. examples in fish: MacKaye & MacKaye 1977; Baylis 1981). The adaptive significance of egg adoption, if any, is puzzling. It may be preferable to leaving a foreign egg near the nest as an attraction to predators, who might then depredate the nest (Tinbergen et al. 1967). All females with small or large total clutch sizes adopted experimental eggs, but half of those with intermediate-sized nests left the egg outside their nest (Table II). It is not clear how to interpret this clutch size relationship. Most nests with six or seven eggs in 1977 probably contained parasitic eggs (Lank, Cooche, Rockwell & Cooke, unpublished data). Thus those with large clutches demonstrated a tendency towards egg acceptance or adoption. This argument cannot explain egg adoption by geese with small clutches. Small clutches have a significantly higher probability of total nest failure than modal or larger-sized clutches (Rockwell et al. 1987), and egg adoption may decrease the chance of total nest failure or loss of the attendant's young

in the event of partial nest predation (Cooke et al. 1985).

Nesting and incubation are clearly expensive physiologically in this species (Ankney 1977; Ankney & MacInnes 1978), but the impact on incubation energetics of adding one or several eggs to a clutch of a given size is not known. In analyses of reproductive success, we have failed to find substantial negative effects of nest parasitism on host fecundity or viability (Lank, Rockwell & Cooke, unpublished data). Clutch size manipulations in other species of waterfowl have not shown increases in physiological incubation cost or decreases in egg hatchability, unless clutches are increased to nearly twice their normal size (Andersson & Eriksson 1982; Rohwer 1985). Since a goose's clutch size is limited (Ryder 1970; Ankney & MacInnes 1978), each egg produced is extremely valuable, and it is unlikely that parasitized females reduce their own clutch size (Andersson & Eriksson 1982; but see Rohwer 1984). At the brood stage, larger family size provides an advantage to parents and young in social encounters (Raveling 1970; Gregoire 1985; but see Lessells 1986 for a short-term cost of increased brood size to adults), or through dilution of predation risk to the parent's own goslings (Hamilton 1971; Nudds 1980; Eadie & Lumsden 1985). In summary, a number of potential advantages may outweigh small increases in incubation costs, and the net effect of egg-adoption on the reproductive success of a female may be nil or even positive.

## Extra-pair Copulation and Fertilization

In contrast to nest parasitism, where the consequences for the attendants are unclear, the gain or loss of even a single fertilization substantially changes a male's annual reproductive output. The behaviour of a nesting male reflects his reproductive defence priorities (sensu Martin 1984). By confronting the intruding male away from the nest, he restricts the possibility of extra-pair copulation with his mate, despite the increased risk of nest parasitism.

Males of many species have been found to time extra-pair copulations so as to maximize the probability of egg fertilization (Beecher & Beecher 1979; Afton 1985; Birkhead et al. 1985; Emlen & Wrege 1986; Birkhead et al. 1987). Observations of male snow geese did not show this pattern (Mineau & Cooke 1979a); however, the sampling was biased

towards events occurring at nest sites. Further observations away from nest sites prior to and during egg laying would be needed to determine whether the temporal distribution documented is in fact representative. The apparent lack of this relationship in snow geese has been taken as evidence that males cannot assess the fertilizability of females (Birkhead & Biggins 1987), and caused other authors to question whether or not the behaviour was actually a reproductive tactic of males (Mineau & Cooke 1979a; Afton 1985; see also Morton 1987). This paper provides clear evidence of a reproductive function.

A male's pursuit of extra-pair copulations is constrained by the primary tactic of mate guarding. In some species, male–male dominance correlated positively with individual extra-pair copulation rate (Birkhead et al. 1985; Frederick 1987). While pursuit of extra-pair copulations might detract from mate guarding, mates of males with high extra-pair copulation rates may in fact be subject to fewer extra-pair copulations (Frederick 1987). In snow geese, early-nesting males will be able to mate-guard early and pursue extra-pair copulation later in the season, and late-nesting females will theoretically be more vulnerable to extra-pair copulation. Once females finish laying, males become less attentive (Mineau & Cooke 1979b) and have more opportunity for extra-pair copulation. The temporal pattern of extra-pair copulations during the breeding season may primarily reflect an increasing operational sex ratio (Birkhead & Biggins 1987).

While mating shows strong positive assortment by morph in this species (Cooke et al. 1976), extra-pair copulation does not. Since family colour affects mate choice (Cooke & McNally 1975), colour mismatches due to extra-pair copulation, like those due to parasitism, will break down the reproductive isolation of the morphs (Cooke 1978; Ford 1983).

All the extra-pair copulations observed to date have been forced on females by males, often neighbours, and may involve direct risks to the female or her eggs (Fujioka & Yamagishi 1981; Werschkul 1982; but see Frederick 1987). While Mineau & Cooke (1979a) is frequently cited in this context, we did not observe egg breakage during extra-pair copulation. While females do not appear to benefit materially through extra-pair copulation, they may benefit through increased genetic variability of offspring. Whether such payoffs exist

for low-fecundity species is controversial (Williams 1975; Maynard Smith 1978). In species that form new pairs each year, individuals will automatically diversify the genetic content of their offspring, but in those with long-term pair bonds, like geese, extra-pair copulations are the only route available for diversifying offspring.

### The Evolution of Intraspecific Nest Parasitism

Data from geese support the hypothesis that coloniality favours higher levels of nest parasitism (see Introduction). Since brood size at hatch averaged around four during this study (Cooke et al. 1985), a rate of 5·64% parasitic goslings suggests that 15–22% of nests were successfully parasitized. The total percentage of parasitized nests was higher than this, since nests with parasitic eggs that failed to hatch are not included. In comparison, intraspecific nest parasitism was detected in 6% of the nests of emperor geese, *Anser canagica*, a semi-colonial species (Eisenhauer & Kirkpatrick 1977), but at only 1% or fewer of the nests in other, non-colonial geese (e.g. MacInnes et al. 1974; Owen & Wells 1979).

Two current hypotheses accounting for the relatively frequent occurrence of nest parasitism in waterfowl do not apply to lesser snow geese. Large clutch size has been suggested as one factor (Yom-Tov 1980; Andersson 1984), but snow geese have small and limited clutches relative to other waterfowl species. Andersson (1984) suggested that female-biased philopatry in waterfowl, including snow geese (Cooke et al. 1975), could promote the spread of intraspecific nest parasitism via kin-selection (Hamilton 1964; Emlen & Wrege 1986). Conditions for the evolution of an altruistic trait by kin selection could be met when the coefficients of relatedness are quite low, if the costs to donors are also low (West-Eberhardt 1975). Parental care in snow geese extends through the first year of life (Prevett & MacInnes 1980), thus there is a reasonable basis for kin-recognition. Attendants might defend nest sites less vigorously if the intruder were an offspring from a previous year, increasing the probability of parasitism of relatives. If parasitism were biased towards kin, however, positive assortative parasitism by morph would be expected. Our finding of randomness with respect to colour is at odds with the maintenance of a substantial kin bias, although the spread of egg adoption might have been initially favoured in this way. Biochemi-

**Table V.** The percentage of young attributed to extra-pair copulation in pair-bonded birds

| Species | Social system | Percentage of excluded young | No. of young | Estimation technique | Source |
|---------|---------------|------------------------------|--------------|----------------------|--------|
| Lesser snow goose | Colonial, monogamy | 2·4 | 50815 | Mendelian genetics | This study |
| Mallards, *Anas platyrhynchos* | Mate defence, monogamy | 5·5–6·9 | 298 | Multiple allozymes | Evarts & Williams 1987, personal communication |
| White-fronted bee-eater, *Merops bullockoides* | Colonial, cooperative monogamy | 1·5 | 97 | Multiple allozymes | Wrege & Emlen 1987 |
| Swallow, *Hirundo rustica* | Colonial, monogamy | 23·6 | 320 | Morphological heritability | Møller 1987a, personal communication |
| Eastern bluebird, *Sialia sialis* | Territorial or colonial, monogamy | 10 | 100 | Multiple allozymes | Gowaty, personal communication |
| Pied and collared flycatchers, *Ficedula hypoeleuca* and *F. albicollis* | Poly-territorial, polygyny | 24 | Ca. 2500 | Morphological heritability | Alatalo et al. 1984 |
| Indigo bunting, *Passerina cyanea* | Territorial, monogamy | 34·7 | 257 | Multiple allozymes | Westneat 1987a |
| White-crowned sparrow, *Zonotrichia leucophrys* | Territorial, monogamy | 34–38 | 110 | Multiple allozymes | Sherman & Morton, in press |

cal studies (e.g. Quinn et al. 1987) provide the most precise method of directly addressing the relatedness of parasites and hosts.

**Extra-pair Fertilization Rates in Birds**

A mixed male reproductive strategy (sensu Trivers 1972) of mate guarding and extra-pair copulation has now been recognized in numerous avian species (Birkhead et al. 1987). Extra-pair copulation has extensive consequences for social organization, promoting mate guarding and extensive time investment by males to protect their paternity (Ford 1983; Mock 1983; Parker 1984; Wrangham & Rubenstein 1986; Birkhead et al. 1987). If extra-pair copulations are not randomly distributed among males and nests, the variance in male reproductive success in socially monogamous species will increase (Trivers 1972; Maynard Smith 1977; Birkhead et al. 1985; Gowaty 1985; Frederick 1987; Westneat 1987a, b).

The ratio of observed pair versus extra-pair copulations has been reported for a number of species (Gladstone 1979; Birkhead et al. 1987; Frederick 1987), but these ratios may not predict the proportion of paternally excluded young (Westneat 1987a). There are a small but growing number of estimates of the proportion of fertilizations attributable to extra-pair copulations in populations of pair-bonded birds (Table V). Table V emphasizes several points. Extra-pair fertilization must now be accepted as a significant influence on the genetic compositions of some natural bird populations. A reproductive function for extra-pair copulation is no longer in doubt (e.g. Mineau & Cooke 1979a; Burns et al. 1980). Finding fertile young when attendant males were sterilized (e.g. Bray et al. 1975) is probably not, as suggested by some, the result of unusual female behaviour induced by male sterility. The logic behind a highly indirect approach using heritabilities (Alatalo et al. 1984), and the implications of the first biochemical demonstrations of mixed paternity within broods (Gowaty & Karlin 1984; Gavin & Bollinger 1985) have been substantiated.

The studies in Table V suggest that coloniality may not promote extra-pair fertilization (Westneat 1987a), a common assumption (see Introduction). While opportunities for extra-pair copulation are

higher in colonial than in non-colonial species, mate guarding (Birkhead 1978; Møller 1985, 1987c; Frederick 1987) or pair copulation rates (Birkhead et al. 1987) may also increase, and the net effect on fertilization success may be nil. However, comparable colonial and non-colonial species will have to be studied, or within-species comparisons will have to be made, before valid conclusions may be drawn. We do not know yet whether the 2·6% extra-pair fertilization rate found for lesser snow geese is high for geese. Alatalo et al. (1984) attributed the high level of extra-pair fertilization detected in flycatchers to their polyterritorial social system, but such an attribution may have been premature.

The eight estimates presented were derived from three different techniques: our Mendelian genetics analysis, multiple-locus allozyme studies (Gowaty & Davies 1986; Wrege & Emlen 1987; Westneat et al. 1987), and estimates from morphological heritability. We used information from a single locus with two alleles and information from homozygous pair types only, and we could not distinguish between homozygous and heterozygous offspring. Nonetheless, our approach had power because: the ease of phenotypic assessment of both adults and offspring made the collection of large amounts of data possible, our allele frequencies of about 0·8 b and 0·2 B were within the range most informative for detecting parental exclusions (Barrowclough et al. 1985; Mumme et al. 1985; Westneat et al. 1987), and assortative mating by colour (Cooke & Cooch 1968) and the existence of only two alleles made homozygous recessive and homozygous pairs quite frequent. A fourth technique, use of restriction fragment length DNA polymorphisms, has tremendous potential in this area (Burke & Bruford 1987; Quinn et al. 1987; Wetton et al. 1987), but there are as yet no avian population studies using the technique. Researchers should consider whether any of these methods are available to them in attacking this question.

## ACKNOWLEDGMENTS

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