

ADOPTION OF YOUNG AND INTRASPECIFIC NEST PARASITISM IN BARNACLE GEESE¹

SHARMILA CHOUDHURY

*The Wildfowl and Wetlands Trust, Slimbridge, GL2 7BT, U.K., and EGI,
Department of Zoology, University of Oxford, Oxford OX1 3PS, U.K.*

CATHERINE S. JONES²

EGI, Department of Zoology, University of Oxford, Oxford OX1 3PS, U.K.

JEFFREY M. BLACK

The Wildfowl and Wetlands Trust, Slimbridge, GL2 7BT, U.K.

JOUKE PROP

*The Wildfowl and Wetlands Trust, Slimbridge, GL2 7BT, U.K., and
Zoological Laboratory, University of Groningen, Haren, The Netherlands*

Abstract. Prior to use of genetic techniques, extra-pair copulations and intraspecific brood parasitism were rarely observed in long-term monogamous geese. DNA fingerprinting analysis of nine families of Barnacle Geese (*Branta leucopsis*) revealed one case of intraspecific nest parasitism with the offspring fathered by the attendant male, and one adoption of a foreign gosling. Observations showed that adoptions accounted for 5.8% and 24.6% of goslings hatched, or 13.3% and 24% of families in two successive years. Adoption appears to be common shortly after the young have hatched and has been assumed to result from accidental brood mixing when parent-offspring recognition is not yet fully developed. We found adoptions to occur in goslings as old as 4–12 weeks, when both parents and offspring are capable of recognizing each other, suggesting that accidental mixing alone cannot explain this phenomenon.

Key words: *Branta leucopsis*; geese; adoption; brood parasitism; extra-pair copulations; DNA fingerprinting.

INTRODUCTION

Species with monogamous mating systems were long thought to have exclusive access to their mates and be assured of the maternity or paternity of their offspring. It is now known that in many such species, animals may rear offspring which are not their own. This occurs either through extra-pair fertilizations or intraspecific brood parasitism. Extra-pair copulations (EPCs) were known to occur in some bird species, but it is only since the advent of genetic analyses using DNA fingerprinting that there is reliable evidence that EPCs can lead to extra-pair paternity (Birkhead et al. 1990, Lifjeld et al. 1991, Smith et al. 1991). Similarly, intraspecific brood parasitism (ISBP) or egg-dumping were suspected in cases of unusually large clutches or deviant

egg laying sequences (Yom-Tov 1980), but only DNA analysis has been able to convincingly detect offspring of foreign origin (Quinn et al. 1987, Birkhead et al. 1990).

Successful EPCs and ISBPs may result in parental resources being provided to non-kin and have major effects on the costs and benefits of parental care, individual fitness, and the success of different mating strategies. To understand avian social organizations, better knowledge is needed of the alternative mating strategies used by birds and their relative success in terms of genetic input into the population. Increased levels of ISBPs and EPCs have been attributed to colonial-living species (Hamilton and Orians 1965, Birkhead 1978, Møller 1987), but appear to be rare in most goose species (McKinney et al. 1984, Lamprecht 1989, Lank et al. 1989, Welsh and Sedinger 1990; but see Lamprecht and Buhrow 1987). Genetic analysis to determine parentage has, however, only been conducted on one species, *Chen caerulescens* (Quinn et al. 1987, Lank et al. 1989).

¹ Received 6 January 1993. Accepted 26 May 1993.

² Present address: Genetic Laboratory, Department of Biochemistry, University of Oxford, Oxford OX1 3PS, U.K.

This paper describes genetic parentage analyses of wild Barnacle Geese *Branta leucopsis*. Barnacle Geese are a long-term monogamous and colonially nesting species. Young are precocial, but stay with their parents for a prolonged period of time, for up to 11 months. The goslings benefit from increased time for feeding due to parental vigilance and protection from conspecific aggression (Black and Owen 1984, 1989a, 1989b). Since parents show prolonged parental care, assured paternity of the offspring might be an important aspect determining the degree of parental care.

METHODS

STUDY POPULATION

A regular banding and observational scheme is carried out on the wild Svalbard population of Barnacle Geese by the Wildfowl and Wetlands Trust, United Kingdom. Birds are caught and marked with individually coded plastic bands most years to maintain about 20–25% of the population banded (see Owen and Black 1989). The coded bands can be read with a telescope from distances up to 250 m, and individuals are resighted 5–8 times a year. At each sighting, observers record the mate, family members and other associations (Owen et al. 1988).

In the summer of 1989, blood samples and observational data were collected from a colony of about 150 geese breeding at Ny Ålesund, Spitsbergen. Blood was obtained from nine families, including nine putative fathers, eight putative mothers, and 18 goslings. Blood (ca. 100–500 μ l) was taken from the brachial vein and placed in 2% SDS, 50 mM EDTA, 50 mM Tris buffer (Griffiths, in press) and frozen at -20°C until analysis. All breeding adults and goslings were released together to prevent family break-up. After being released, marked birds were observed for two days and family compositions recorded. Birds were resighted after migration to the wintering grounds in Scotland, and family compositions were recorded again.

DNA-FINGERPRINTING

DNA was extracted by resuspending 100 μ l of blood solution in 500 μ l STE buffer (0.1 M Tris-HCl, pH 8.0, 0.1 M NaCl, 1 mM EDTA), 10 μ l Proteinase K (10 mg/ml), and 20 μ l of 25% SDS, and incubating overnight at 37°C . The samples were extracted twice with equal volume phenol/chloroform and once with chloroform/isoamyl

alcohol (24:1). DNA was precipitated with absolute ethanol, washed with 70% ethanol, vacuum dried, and re-dissolved overnight in 300 μ l TE buffer (10 mM Tris-HCl, pH 7.5, 1 mM EDTA). The concentrations of total genomic DNA were determined by ethidium bromide fluorescence by comparison with known standards, and approximately 5 μ g DNA was digested with 20 units HaeIII restriction endonuclease, in the presence of 4 mM spermidine trichloride to facilitate complete digestion, for about 16 hr at 37°C . Digested DNA was extracted with phenol/chloroform, precipitated with absolute ethanol, washed with 70% ethanol, vacuum dried, and dissolved in 50–100 μ l TE.

Digested DNA was calibrated using a Hoefer TKO-100 DNA Fluorometer, and approximately 10 μ g DNA were loaded into each gel track with $1 \times$ ficoll loading buffer (Sambrook et al. 1989). The samples were electrophoresed through a 30 cm long 1.0% agarose gel in $1 \times$ TBE buffer (0.089 M Tris-base, 0.089 M boric acid, 0.002 M EDTA, pH 8.3), at approximately 1.5V/cm until the 2 KB marker (λ HindIII) was about 6 cm from the end of the gel (ca. 40 hr). After electrophoresis, DNA was dephosphorylated with two washes of 0.25 M HCl (15 min each), denatured in two washes of 0.5 M NaOH, 1.5 M NaCl (30 min each), and neutralized with two washes of 1.5 M NaCl, 0.5 M Tris-HCl, pH 7.2, 0.001 M EDTA (20 min each). The Southern blotting technique (Southern 1975) was used to transfer the DNA to Zeta-probe GT nylon membranes (Biorad), subsequently the membrane was rinsed briefly in $2 \times$ SSC, and the DNA was fixed by air-drying the filter in an 80°C oven for a minimum of 30 min.

Filters were prehybridized for 3 hr at 65°C , using the method of Westneat et al. (1988), and then hybridized in the same solution with the addition of radioactively labeled probes for 24–36 hr at 65°C . Two different 32P -labeled probes were used: Jeffreys 33.15 and 33.6 probes (Jeffreys et al. 1985). The probes were obtained by random priming of single-stranded M13 DNA with either 33.15 or 33.6 inserts with 32P (Feinberg and Vogelstein 1983, 1984). Probed filters were washed once in 0.25 M sodium phosphate, 1% SDS (15 min), twice in $2 \times$ SSC, 0.1% SDS (25 min each), and then repeatedly in $1 \times$ SSC, 0.1% SDS (25 min each) at 65°C , until blank control filters showed only background radiation levels. Autoradiographs of varying exposure and

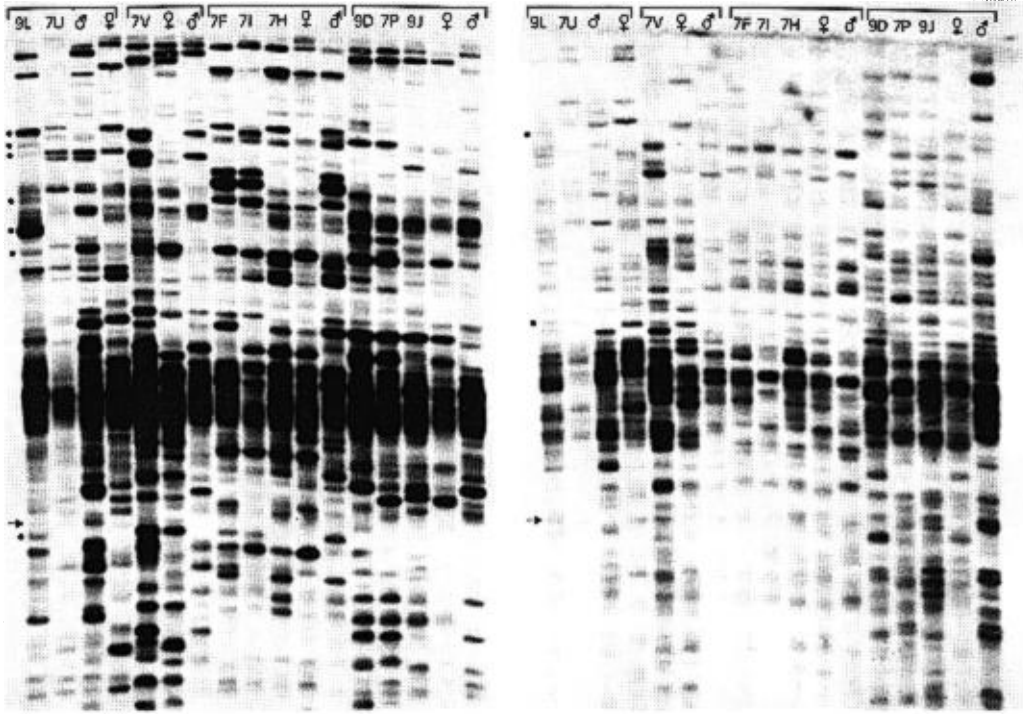


FIGURE 1. DNA fragments of four families of Barnacle Geese (families indicated by brackets), using Jeffreys 33.15 (left hand plate) and 33.6 probes (right hand plate). The 2.0 kilobase marker (derived from lambda DNA digested with Hind III) is indicated by an arrow. All offspring, with the exception of one (9L, track 1), can be correctly assigned to the putative parents. Offspring 9L was illegitimate with respect to the putative mother and several obviously mismatched bands are indicated (●).

sharpness were obtained for each probed filter, by exposure to Kodak X-Omat film in X-ray cassettes for 1–14 days at -70°C , with one or two intensifying screens. Each filter was probed once with 33.15 and once with 33.6, so as to obtain two fingerprints for each individual.

FINGERPRINT ANALYSIS

Electrophoresis in the DNA fingerprinting technique separates DNA fragments by molecular weight, and each fragment or band in an offspring should appear in one of its two parents. Acetate overlays were used to mark the positions of bands when scoring the fingerprints using methods described by Galbraith et al. (1991). Bands were scored on the basis of distance migrated down the gel and intensity of the band, since similar concentrations of DNA were loaded into each track. A combination of two band scoring methods was used to analyze parentage: (1) novel fragments and (2) band sharing coefficients. Novel fragments in an offspring, i.e., fragments not occurring in either parent, can arise either by mu-

tation, or if one or both putative parents are not the genetic parents (Burke 1989). Mutations can generally explain a low frequency of novel fragments, the exact number depending upon the species' natural mutation rate (Jeffreys et al. 1987, Gyllensten et al. 1990), but a large number of unassigned bands are likely to be due to EPCs or ISBPs. Novel fragments alone, however, are unable to indicate which parent is unrelated to the offspring. Bandsharing coefficients between offspring and parents are able to resolve this. The band-sharing coefficient between two individuals was calculated as twice the number of shared bands divided by the total number of bands in both individuals (Wetton et al. 1987). Since offspring inherit half their genotype from each parent, band-sharing with real parents should approximate 50%.

RESULTS

VARIABILITY

Autoradiographs from the two probes revealed considerable individual variation in banding

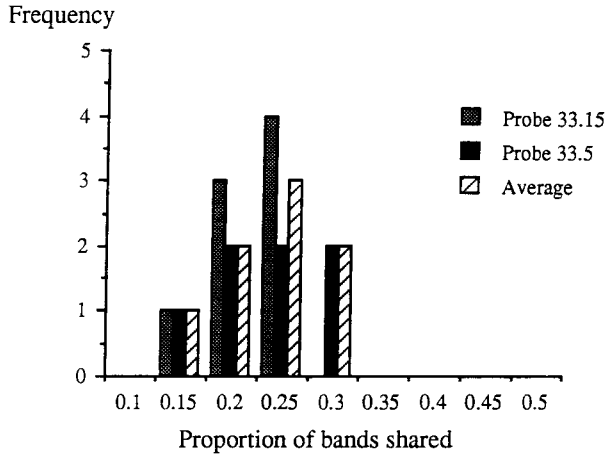


FIGURE 2. Distribution of proportion of bands shared between unrelated adults.

patterns. Each probe provided a different set of bands for the same individual, with little overlap (Probe 33.15: mean bands = 25.8, SD = 5.3, $n = 35$; Probe 33.6: mean bands = 22.1, SD = 8.0, $n = 35$). Each probe presumably detects a different set of hypervariable minisatellites, which increases the amount of genetic variation assayed and the probability of assigning parentage correctly (Jeffreys et al. 1985, 1986; Westneat 1990). For both probes, most of the scorable bands were larger than 2 KB (approximately 80%) (Fig. 1).

Background band-sharing level was calculated from the number of bands shared by mates, assuming that mates are unlikely to be related. We also assumed that there was no significant linkage between bands, because we did not have large enough families for a segregation analysis (Burke et al. 1991). Both probes gave similar background band-sharing coefficients (Probe 33.15:

0.20, Probe 33.6: 0.25; $t = 1.13$, $df = 8$, $P = 0.29$), therefore an average background band-sharing coefficient of 0.23 was used. Figure 2 shows the frequency distributions of band-sharing estimates between mates for each probe, as well as a combined average.

ANALYSIS OF PARENTAGE

The number of novel fragments of each offspring was determined by combining scores from both probes. Of 16 goslings for which samples from both putative parents were available, eight had no unassigned bands, six had fewer than three novel fragments, and two had 14 and 19 novel bands respectively (Fig. 3). Since there is a distinct bimodal distribution of offspring with few and many novel fragments, we assume that the few unassigned bands are due to mutation (Jeffreys et al. 1985) and that many novel bands are

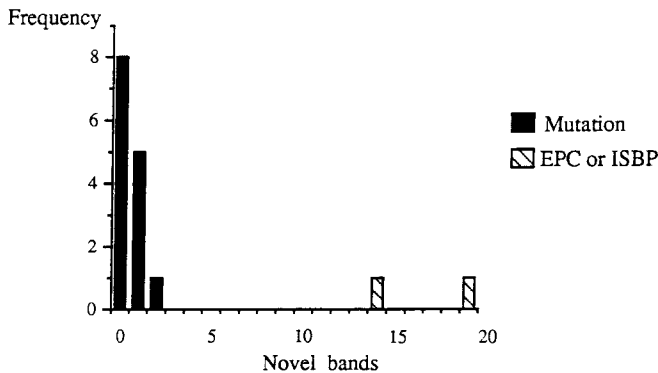


FIGURE 3. Distribution of offspring with different number of novel fragments.

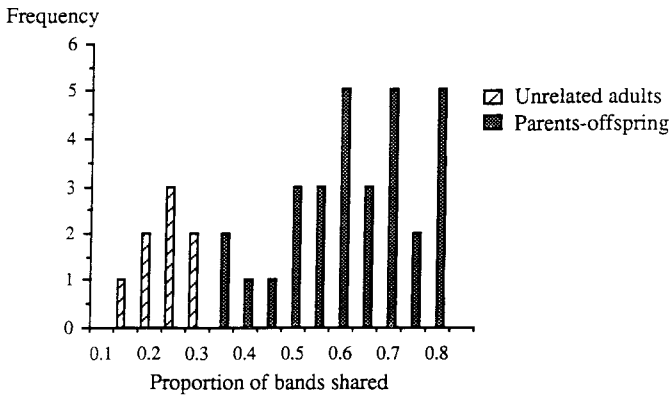


FIGURE 4. Distribution of band-sharing coefficients of related and unrelated individuals.

the result of EPCs or ISBPs. Using offspring with 0–2 novel fragments, the natural mutation rate (m) in the species was estimated, where $m = M/(N \cdot n)$, and M is the number of novel bands, N the number of offspring examined, and n the mean number of bands per fingerprint. The estimated mutation rates from the two probes varied slightly (Probe 33.15: $m = 0.0138$; Probe 33.6: $m = 0.0065$), but the average rate using novel fragments from both probes was 0.0104 and is very similar to that found in other bird species (Burke and Bruford 1987, Westneat 1990, Jones et al. 1991).

Goslings with fewer than three novel fragments were used to determine parent-offspring band-sharing distributions. There was no significant difference between the two probes ($t = 0.85$, $df = 50$, $P = 0.40$), therefore band-sharing coefficients were averaged. Mean band-sharing for parent to offspring was 0.62 (SD = 0.12; $n = 14$), and there was no significant difference between band-sharings of fathers and mothers with offspring ($t = 0.27$, $df = 24$, $P = 0.79$). Although the range of band-sharing coefficients is large (0.33–0.79), the distribution of band-sharings between parent-offspring is distinct from the distribution of unrelated adults (Fig. 4).

One gosling (9F) with a large number of unassigned bands (19) had extremely low band-sharing coefficients with both putative mother (0.27) and putative father (0.25). This could be a case of egg-dumping, but behavioral data suggests an alternative explanation. On the breeding grounds, the family had five goslings, but 9F was not among them. When resighted on the wintering grounds two months later, the family had

lost two offspring and gained two new ones, one of the new goslings being 9F. The two new goslings were presumably adopted by the family either shortly prior to or shortly after migration from the arctic breeding grounds, i.e., when they were about 4–12 weeks old.

Adoption has been widely reported in geese (see Glasgow 1977 and Eadie et al. 1988 for reviews), but there have been few attempts to quantify it. We ascertained how common adoption of foreign goslings may be in Barnacle Geese from resighting records at the Diabas colony on Spitsbergen in 1980–1981 (Table 1). We defined adoption as an increase in brood size between successive observations of banded parents. Adoption was most common on the nesting island when goslings were a few days old (involving 13.3% of families and 5.8% of goslings in 1980; 24% of families and 24.6% of goslings in 1981), especially in poor weather when several families were waiting to leave the island for the mainland tundra. On the mainland, adoptions still occurred, but were less frequent (1.3% of families and 0.4% of goslings in 1980; 4% of families and 3% of goslings in 1981). The age of broods adopting goslings on the mainland ranged from 20–28 days. The mean proportion of families that adopted foreign goslings over both years was 18%, and the mean percentage of adopted goslings was 10.8%. These figures only include successful adoptions, but there were many cases where orphan goslings attempted to join families, were repeatedly chased away by the adults, and subsequently taken by gulls.

The gosling with 14 novel fragments (9L, Fig. 1, track 1), shared few bands with the mother

(0.34) and a higher proportion with the father (0.51). Although the band-sharing coefficient with the mother is at the distribution boundary of related and unrelated individuals (Fig. 4), the high number of novel fragments indicates a different genetic parent. This suggests the offspring was fathered by the nest-holding male, but had a different mother. The parental male may have engaged in an EPC with another female, who subsequently dumped an egg into the nest of the pair. Alternatively, the male may have had a secondary female who did not nest herself, but laid into the nest of the primary female (Weigmann and Lamprecht 1991; Choudhury and Black, in press).

DISCUSSION

Prior to the use of genetic techniques, behavioral observations suggested that EPCs and ISBPs are rare in most geese (McKinney et al. 1983, 1984; Andersson 1984). Our findings from DNA fingerprinting analyses of Barnacle Goose families support the conclusions from the few other genetic studies that alternative reproductive strategies of geese may be quite effective (Quinn et al. 1987; Lank et al. 1989; Tegelstrom, pers. comm.). In nine Barnacle Goose families, we found one adoption of a foreign gosling and one case of egg-dumping, with the offspring related to the nesting father but not the mother. Although there was no evidence of EPCs involving the females in the families fingerprinted, we detected a dumped egg fathered by the host male, which suggests that the male may have been involved in an EPC with another female. Alternatively, the male may have had a secondary female, who laid her egg in the nest of the primary female. Secondary females are tolerated much closer to the nest than other birds (Lamprecht and Buhrow 1987; Choudhury and Black, in press), and may have a fairly high chance of successfully parasitizing the primary female's nest.

Adoption of young after hatch has been described in at least 28 species of waterfowl, including a number of goose species (Glasgow 1977; Pevett and MacInnes 1980; Zicus 1981; Williams, in press). We found that adoption of foreign goslings could affect up to 25% of goslings hatched and 24% of families. Brood mixing occurs when a pair loses or abandons its young to another pair, who subsequently foster the young as their own. In precocial species, particularly colonial nesting ones, there is the risk of young

TABLE 1. Exchange of goslings between broods at Diabas colony, Spitsbergen (1980/1981).

	1980	1981
Total number of families	75	25
Total number of goslings	240	65
Mean brood size	3.2	2.6
On nesting island		
Number of families adopting goslings	10	6
Number of adopted goslings	14	16
On mainland tundra		
Number of families adopting goslings	1	1
Number of adopted goslings	1	2

losing their parents and attempting to join other families. This may be particularly so, during the first days after hatch, when parent-offspring recognition is not strengthened yet by mutual association (Collias and Jahn 1959, Hanson 1965, Sherwood 1966, Glasgow 1977). If adoption is caused by accidental brood mixing due to errors in kin-recognition, we predict that it will be restricted to the period shortly after hatch. In domestic geese, parents recognize their young by about 15 days (Ramsey 1951) and in Snow Geese by about 10 days after hatch (Pevett and MacInnes 1980). In Barnacle Geese, adoptions occurred mainly in the first few days after hatch, particularly while families were waiting to move from the nesting island to the mainland feeding sites, but brood mixing also occurred with goslings as old as 4–12 weeks of age. Similarly, Zicus (1981) found that 35% of adoptions in Canada Geese (*Branta canadensis*) occurred at over 21 days of age. Williams (in press) studied 982 broods of Lesser Snow Geese and found that adoption occurred in a minimum of 13% of broods, with 46% of broods adopting goslings 15–30 days after the mean hatch date. This suggests that adoptions are common even after parent-offspring recognition is well-developed and that accidental separation alone cannot explain adoption in geese.

For a lost offspring, it is advantageous to join another family as soon as possible. Predation is highest in the first two weeks of life (MacInnes et al. 1974, Prop et al. 1984) and parental protection is likely to play a significant role in offspring survival (Black and Owen 1987). Williams (in press) found that once a gosling was adopted, it had an equal chance of survival as other gos-

lings in the brood. In addition, family goslings have a distinct advantage over unattached goslings in that they have access to the better foods, are attacked and displaced less frequently, are able to feed without interruption for longer periods, and gain more weight (Black and Owen 1984, 1989a, 1989b). Although adoption is clearly adaptive for goslings, we would expect foster parents to incur increased costs in terms of reduced future fitness and survival, and hence to reject foreign goslings. This suggests that either (1) being parasitized entails little cost, (2) discriminating against foreign offspring is very costly, or (3) being parasitized has some benefits.

In arctic-nesting geese, parental investment appears to be greatest during the early stages of reproduction, i.e., egg laying and incubation (Ankney 1977, Ankney and MacInnes 1978). However, there is little evidence that the addition of one or several eggs to a clutch has significant negative effects on hatching success of the young (Lessells 1986; Rockwell et al. 1987, but see Weigmann and Lamprecht 1991) or host fecundity or viability (Lank et al. 1989, but see Lessells 1987 and Schindler and Lamprecht 1987). Compared with altricial species that have to feed their young, precocial birds such as geese invest proportionately less in the post-hatch care of young. Parental care following hatching consists mainly of vigilance for predators, aggressive interactions with conspecifics, and food-sharing (Lazarus and Inglis 1978; Black and Owen 1989a, 1989b; Seding and Raveling 1990).

Lazarus and Inglis (1986) proposed that when parental investment is "unshared" among brood members, that is, when benefits experienced by one offspring do not diminish benefits experienced by other brood members, there should be no relationship between investment and brood size. Thus, in geese, where parental vigilance or protection can serve all brood members equally, acceptance of additional offspring may have little negative effect on the host family (Lazarus and Inglis 1978; Lessells 1987, but also see Schindler and Lamprecht 1987 and Seding and Raveling 1990). In some cases, the acceptance of additional young into the family may actually carry benefits to the host family. Cooch et al. (1991) showed that goslings in larger broods of Lesser Snow Geese had faster growth rates than those in smaller broods. Additional foster young may dilute the risk of predation to the parents' own offspring in larger broods, as well as facilitate

rapid detection of predators (Eadie and Lumsden 1985, Eadie et al. 1988). Black and Owen (1989a) suggest that prolonged parent-offspring association in geese is facilitated by goslings increasingly helping parents in sharing the vigilance burden and assisting in conflicts with neighbors. Dominance rank and access to limiting resources is determined by the size of the social unit in geese, so that the presence of young helps to raise the rank of the family as a whole (Raveling 1970, Lamprecht 1986). Lamprecht (1986) observed that pairs adopting young after failing to hatch their own, ranked as high as normal families, and Gregoire and Ankney (1990) found that large families of Lesser Snow Geese dominated smaller families on the wintering and spring staging grounds. We suggest that in geese, the costs of being parasitized may be low, while a large family size may have some advantages. Hence, there may be little incentive to evolve mechanisms to discriminate against foreign eggs. Also, if the costs of developing kin discrimination mechanisms are higher than the costs of being parasitized, selection will not favor kin discrimination (Barnard and Aldous 1991).

ACKNOWLEDGMENTS

We thank the Wildfowl & Wetlands Trust staff who helped with the capture of geese at Ny Ålesund and the resighting of birds in winter 1989–1990. We are grateful to Peter Holland at Oxford for the use of his laboratory and his support, and to Chris Perrins, Ben Hatchwell and Jürg Lamprecht for commenting on earlier drafts of the manuscript. S. Choudhury was funded by the Wildfowl & Wetlands Trust, Moorgate Trust, Mitchell Trust, Alan Evans Memorial Trust and Loke Wan Tho Memorial Foundation. C. S. Jones was supported by a NERC post-doctoral assistantship.

LITERATURE CITED

- ANDERSSON, M. 1984. Brood parasitism within species, p. 195–228. *In* C. J. Barnard [ed.], *Producers and scroungers*. Chapman and Hall, New York.
- ANKNEY, C. D. 1977. The use of nutrient reserves by breeding male Lesser Snow Geese *Chen caerulescens caerulescens*. *Can. J. Zool.* 55:1984–1987.
- ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459–471.
- BARNARD, C. J., AND P. ALDOUS. 1991. Kinship, kin discrimination and mate choice, p. 125–147. *In* P. Hepper [ed.], *Kin recognition*. Cambridge Univ. Press, Cambridge.
- BIRKHEAD, T. R. 1978. Behavioural adaptation to high density in the Common Guillemot *Uria aalge*. *Anim. Behav.* 26:321–331.
- BIRKHEAD, T. R., T. BURKE, R. ZANN, F. M. HUNTER, AND A. P. KRUPA. 1990. Extra-pair paternity and

- intraspecific brood parasitism in wild Zebra Finches *Taeniopygia guttata*, revealed by DNA fingerprinting. *Behav. Ecol. Sociobiol.* 27:315–324.
- BLACK, J. M., AND M. OWEN. 1984. Importance of the family unit to Barnacle Goose *Branta leucopsis* offspring—a progress report. *Norsk. Polarinst. Skr.* 181:79–85.
- BLACK, J. M., AND M. OWEN. 1987. Determinant factors of social rank in goose flocks: acquisition of social rank in young geese. *Behaviour* 102:129–146.
- BLACK, J. M., AND M. OWEN. 1989a. Parent-offspring relationships in wintering Barnacle Geese. *Anim. Behav.* 37:187–198.
- BLACK, J. M., AND M. OWEN. 1989b. Agonistic behaviour in Barnacle Goose flocks: assessment, investment and reproductive success. *Anim. Behav.* 37:199–209.
- BURKE, T. 1989. DNA fingerprinting and other methods for the study of mating success. *TREE* 4:139–144.
- BURKE, T., AND M. W. BRUFORD. 1987. DNA fingerprinting in birds. *Nature* 327:149–152.
- BURKE, T., O. HANOTTE, M. W. BRUFORD, AND E. CAIRNS. 1991. Multilocus and single locus minisatellite analysis in population biological studies, p. 154–168. *In* T. Burke, G. Dolf, A. J. Jeffreys, and R. Wolff [eds.], *DNA fingerprinting: approaches and applications*. Birkhauser Verlag, Basel, Switzerland.
- CHOUDHURY, S., AND J. M. BLACK. *In press*. Mate selection behaviour and sampling strategies in geese. *Anim. Behav.* 45.
- COLLIAS, N. E., AND L. R. JAHN. 1959. Social behaviour and breeding success in Canada Geese (*Branta canadensis*) confined under semi-natural conditions. *Auk* 76:478–509.
- COOCH, E. G., D. B. LANK, A. DZUBIN, R. F. ROCKWELL, AND F. COOKE. 1991. Body size variation in Lesser Snow Geese: environmental plasticity in gosling growth rates. *Ecology* 72:503–512.
- EADIE, J. MCA., AND H. G. LUMSDEN. 1985. Is nest parasitism always deleterious to Goldeneyes? *Am. Nat.* 126:859–866.
- EADIE, J. MCA., F. P. KEHOE, AND T. D. NUDDS. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. *Can. J. Zool.* 66:1709–1721.
- FEINBERG, A. P., AND B. VOGELSTEIN. 1983. A technique for radiolabelling DNA restriction endonuclease fragments to high specific activity. *Anal. Biochem.* 132:6–13.
- FEINBERG, A. P., AND B. VOGELSTEIN. 1984. Addendum—a technique for radiolabelling DNA restriction endonuclease fragments to high specific activity. *Anal. Biochem.* 137:266–267.
- GALBRAITH, D. A., P. T. BOAG, H. L. GIBBS, AND B. N. WHITE. 1991. Sizing bands on autoradiograms: a study of precision for scoring DNA fingerprints. *Electrophoresis* 12:210–220.
- GLASGOW, W. M. 1977. Brood mixing behaviour and population dynamics of Canada Geese at Dowling Lake, Alberta. M.Sc.thesis, Univ. of Alberta, Edmonton, Alberta, Canada.
- GREGOIRE, P. E. AND C. D. ANKNEY. 1990. Agonistic behaviour and dominance relationships among Lesser Snow Geese during winter and spring migration. *Auk* 107:550–560.
- GRIFFITHS, R. *In press*. Sex-biased mortality in the Lesser Black-backed Gull (*Larus fuscus*) during the nesting stage. *Ibis*.
- GYLLENSTEN, U. B., S. JAKOBSSON, AND H. TEMRIN. 1990. No evidence for illegitimate young in monogamous and polygynous warblers. *Nature* 343:168–170.
- HAMILTON, W. D., AND G. H. ORIAN. 1965. Evolution of brood parasitism in birds. *Condor* 67:361–382.
- HANSON, H. C. 1965. *The giant Canada Goose*. Southern Illinois University Press, Carbondale, IL.
- JEFFREYS, A. J., V. WILSON, AND S. L. THEIN. 1985. Hypervariable 'minisatellite' regions in human DNA. *Nature* 314:67–73.
- JEFFREYS, A. J., V. WILSON, S. L. THEIN, D. L. WEATHERALL, AND B.A.J. PONDER. 1986. DNA 'fingerprints' and segregation analysis of multiple markers in human pedigrees. *Am. J. Hum. Genet.* 39:11–24.
- JEFFREYS, A. J., V. WILSON, R. KELLY, B. A. TAYLOR, AND G. BULFIELD. 1987. Mouse DNA 'fingerprints': analysis of chromosome location and germline stability of hypervariable loci in recombinant inbred strains. *Nucleic Acids Res.* 15:2823–2836.
- JONES, C. S., C. M. LESSELLS, AND J. R. KREBS. 1991. Helpers-at-the-nest in European Bee-eaters (*Merops apiaster*): a genetic analysis, p. 169–192. *In* T. Burke, G. Dolf, A. J. Jeffreys, and R. Wolff [eds.], *DNA fingerprinting: approaches and applications*. Birkhauser Verlag, Basel, Switzerland.
- LAMPRECHT, J. 1986. Structure and causation of the dominance hierarchy in a flock of Bar-headed geese (*Anser indicus*). *Behaviour* 96:28–48.
- LAMPRECHT, J. 1989. Mate guarding in geese: awaiting female receptivity, protection of paternity or support of female feeding?, p. 48–66. *In* A. E. Rasa, C. Vogel, and E. Voland [eds.], *The sociobiology of sexual and reproductive strategies*. Chapman and Hall, London.
- LAMPRECHT, J., AND H. BUHROW. 1987. Harem polygyny in Bar-headed Geese. *Ardea* 75:285–292.
- LANK, D. B., P. MINEAU, R. F. ROCKWELL, AND F. COOKE. 1989. Intraspecific nest parasitism and extra-pair copulation in Lesser Snow Geese. *Anim. Behav.* 37:74–89.
- LAZARUS, J., AND I. R. INGLIS. 1978. The breeding behaviour of the Pink-footed Goose: parental care and vigilant behaviour during the fledging period. *Behaviour* 65:62–88.
- LAZARUS, J., AND I. R. INGLIS. 1986. Shared and unshared parental investment, parent-offspring conflict and brood size. *Anim. Behav.* 34:1791–1804.
- LESSELLS, C. M. 1986. Brood size in Canada Geese: a manipulation experiment. *J. Anim. Ecol.* 55:669–689.
- LESSELLS, C. M. 1987. Parental investment, brood size and time budgets: behaviour of Lesser Snow

- Goose *Anser c. caerulescens* families. *Ardea* 75: 189-203.
- LIFIELD, J. T., T. SLAGSVOLD, AND H. M. LAMPE. 1991. Low frequency of extra-pair paternity in Pied Flycatchers revealed by DNA fingerprinting. *Behav. Ecol. Sociobiol.* 29:95-101.
- MACINNES, C. D., R. A. DAVIES, R. N. JONES, B. LIEFF, AND A. J. PAKULAK. 1974. Reproductive efficiency of McConnell River small Canada Geese. *J. Wildl. Manage.* 38:686-707.
- MCKINNEY, F., S. R. DERRIKSON, AND P. MINEAU. 1983. Forced copulations in waterfowl. *Behaviour* 86:250-294.
- MCKINNEY, F., K. M. CHENG, AND D. J. BRUGGERS. 1984. Sperm competition in apparently monogamous birds, p. 523-545. In R. L. Smith [ed.], *Sperm competition and the evolution of animal mating systems*. Academic Press, New York.
- MØLLER, A. 1987. Intraspecific nest parasitism and anti-parasite behaviour in swallows, *Hirundo rustica*. *Anim. Behav.* 35:247-254.
- OWEN, M. AND J. M. BLACK. 1989. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. *J. Anim. Ecol.* 58:603-617.
- OWEN, M., J. M. BLACK, AND H. LIBER. 1988. Pair bond duration and timing of its formation in Barnacle Geese (*Branta leucopsis*), p. 23-38. In M. W. Weller [ed.], *Waterfowl in winter*. Univ. of Minnesota Press, Minneapolis.
- PREVETT, J. P., AND C. D. MACINNES. 1980. Family and other social groups in Snow Geese. *Wildl. Monographs* 71:1-46.
- PROP, J., M. VAN EERDEN, AND R. H. DRENT. 1984. Reproductive success of the Barnacle Goose in relation to food exploitation on the breeding grounds, western Spitsbergen. *Norsk. Polarinst. Skr.* 181:87-117.
- QUINN, T. W., J. S. QUINN, F. COOKE, AND B. N. WHITE. 1987. DNA marker analysis detected multiple maternity and paternity in single broods of the Lesser Snow Goose. *Nature, Lond.* 326:392-394.
- RAMSEY, A. O. 1951. Familial recognition in domestic birds. *Auk* 68:1-16.
- RAVELING, D. G. 1970. Dominance relationships and agonistic behaviour of Canada Geese in winter. *Behaviour* 37:291-319.
- ROCKWELL, R. F., C. S. FINDLAY, AND F. COOKE. 1987. Is there an optimal clutch size in Snow Geese? *Am. Nat.* 130:839-863.
- SAMBROOK, J., E. F. FRITSCH, AND T. MANIATIS. 1989. *Molecular cloning: a laboratory manual*. Second edition. Cold Spring Harbour Laboratory, New York.
- SCHINDLER, M., AND J. LAMPRECHT. 1987. Increase of parental effort with brood size in a nidifugous bird. *Auk* 104:688-693.
- SEDINGER, J. S., AND D. G. RAVELING. 1990. Parental behaviour of Cackling Canada Geese during brood rearing: division of labor within pairs. *Condor* 92: 174-181.
- SHERWOOD, G. A. 1966. *Canada Geese of the Seney National Wildlife Refuge*. Ph.D. diss., Utah State University, Logan, UT.
- SMITH, H. G., R. MONTGOMERIE, T. POLDMAA, B. N. WHITE, AND P. T. BOAG. 1991. DNA fingerprinting reveals relation between tail ornaments and cuckoldry in Barn Swallows, *Hirundo rustica*. *Behav. Ecol.* 2:90-98.
- SOUTHERN, E. M. 1975. Detection of specific sequences among DNA fragments separated by gel electrophoresis. *J. Mol. Biol.* 98:503-517.
- WEIGMANN, C., AND J. LAMPRECHT. 1991. Intraspecific nest parasitism in Bar-headed Geese, *Anser indicus*. *Anim. Behav.* 41:677-688.
- WELSH, D., AND J. S. SEDINGER. 1990. Extra-pair copulations in Black Brant. *Condor* 92:242-244.
- WESTNEAT, D. F. 1990. Genetic parentage in the Indigo Bunting: a study using DNA fingerprinting. *Behav. Ecol. Sociobiol.* 27:67-76.
- WESTNEAT, D. F., W. A. NOON, H. K. REEVE, AND C. F. AQUADRO. 1988. Improved hybridization conditions for DNA fingerprints probed with M13. *Nucleic Acids Res.* 16:4161.
- WETTON, J. H., R. E. CARTER, D. T. PARKIN, AND D. WALTERS. 1987. Demographic study of a wild House Sparrow population by DNA fingerprinting. *Nature* 327:147-149.
- WILLIAMS, T. D. In press. Adoption in a precocial species, the Lesser Snow Goose: intergenerational conflict, altruism or a mutually beneficial strategy? *Anim. Behav.*
- YOM-TOV, Y. 1980. Intraspecific nest parasitism in birds. *Biol. Rev.* 55:93-108.
- ZICUS, M. C. 1981. Canada Goose brood rearing behaviour and survival estimates. *Wilson Bull.* 93: 207-217.