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GENETIC ANALYSIS OF OFFSPRING OF A FEMALE-FEMALE PAIR IN THE LESSER SNOW GOOSE (*CHEN C. CAERULESCENS*)

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ABSTRACT.—We used restriction-fragment-length polymorphism (RFLP) analysis to establish the parentage of a clutch of eight eggs being incubated by two female Lesser Snow Geese to determine if both females had contributed to the clutch, and whether a single male had fertilized both females. Genotypes at 30 polymorphic restriction enzyme sites were surveyed with 14 cloned DNA probes. Sexing of all individuals was done both by dissection and by use of a DNA probe that detected the presence of the W chromosome in females. Paternal genotypes were reconstructed from haplotypes of the offspring. We determined that both females had contributed to the clutch, and that each was fertilized by a different male. *Received 9 May 1988, accepted 30 September 1988.*

THE occurrence of female-female (FF) pairs was first reported in Western Gulls (*Larus occidentalis*) by Hunt and Hunt (1977). Subsequently, such reports have been extended to include Ring-billed Gulls (*L. delawarensis;* Ryder and Somppi 1979, Conover et al. 1979), Herring Gulls (*L. argentatus;* Fitch 1980, Shugart 1980), California Gulls (*L. californicus;* Conover et al. 1979) and Caspian Terns (*Sterna caspia;* Conover 1983). The discovery of FF pairs in these species usually followed initial observations of supernormal clutches (SNCs) in breeding populations.

SNCs can result from a number of different events. If no nest attendants exist, a SNC is likely the result of egg dumping into an abandoned nest, such as observed by Delnicki et al. (1976). If a heterosexual pair is in attendance, the likely explanation is intraspecific brood parasitism (Yom-Tov 1980). If two females are in attendance, presumably both have contributed to produce a SNC.

There are two explanations possible for the presence of two females defending a SNC. The females are either involved in a polygynous group and the male's absence is due to abandonment, death, or infrequent attendance at the nest, or there never was a resident male and the two females can be considered a FF pair by the criterion of Hunt and Hunt (1977). Until now, the most reliable way to distinguish the alternatives was to show that the two females remain paired through two or more breeding seasons in the absence of a resident male (Kovacs and Ryder 1981).

We previously used restriction-fragment-length-polymorphism (RFLP) analysis to detect the occurrence of intraspecific brood parasitism in the Lesser Snow Goose (*Chen caerulescens caerulescens*) (Quinn et al. 1987). This type of genetic analysis makes use of the many polymorphic genetic markers detectable at the DNA level (Quinn and White 1987a, b). Here we used the same type of analysis to assess the parentage of a single SNC which was being incubated by two female Lesser Snow Geese.

METHODS

A colony of Lesser Snow Geese at La Perouse Bay near Churchill Manitoba (58°24'N, 94°24'W) has been

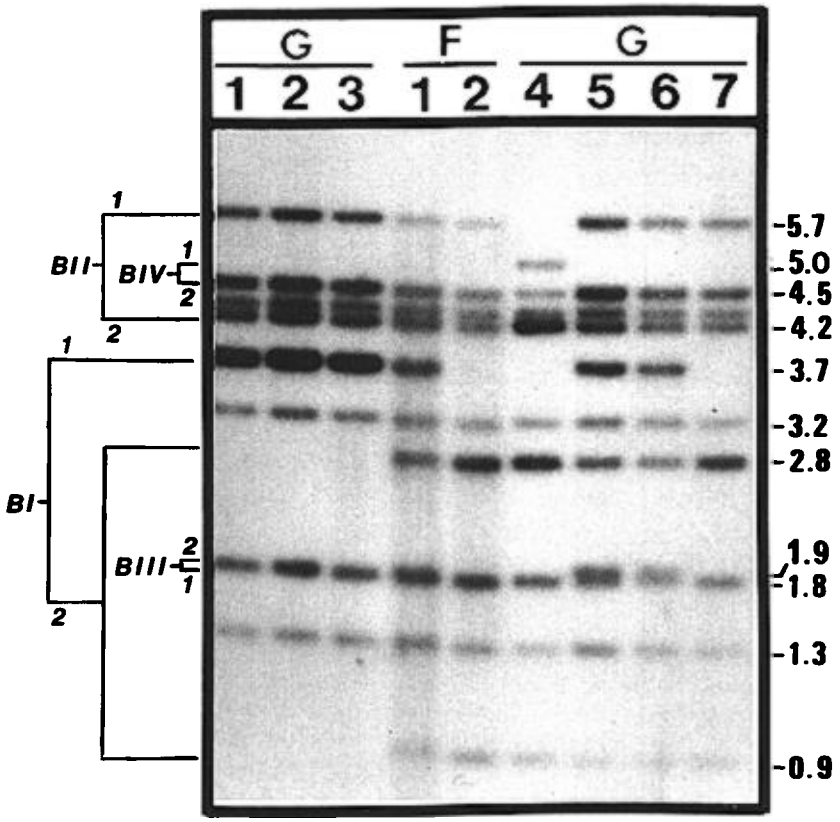

Fig. 1. Autoradiograph supporting the exclusion of F2 as a possible mother of 3 goslings. Polymorphisms at 4 restriction sites (BI-BIV) were detected with DQSG7, as shown on the left. G1, G2, and G3 were all homozygous (BI-[1,1]) for the 3.7 kb band. Because F2 was homozygous (BI-[2,2]) for the alternate bands (2.8 kb, 0.9 kb), F2 was excluded as a possible genetic parent of those three goslings.

the site of a long-term study by Cooke and associates (Cooke 1987). During a routine nest check on 21 June 1985, we observed a pair of nest attendants, both of which had brood patches bordered by yellow-stained feathers (indicative of active brooding). There was no indication of a male in attendance, and when the "pair" was together, there was no excessive mate calling as is typical in Snow Geese when their mate is absent and they are threatened. The nest contained 8 eggs, some of which were in the early hatching stage. We considered this to be a SNC because clutch size in Snow Geese at this colony normally ranges from 2–6 with an average of 4–5 (Cooke 1987) and clutches of 8 are rare (0.5% of completed clutches at La Perouse Bay in 1985), and female Snow Geese have a maximum of 6 postovulatory follicles (Ankney 1978). The following day, the same two attendants were present again with no sign of a male. The nest now contained 3 "fluffy" (dry) goslings (G1–3), 2 damp goslings (G4, 5), 1 wet gosling (G6), 1 pipping egg (G7), and 1 inactive egg which was later found to be addled. When approached, both female nest attendants (F1 and F2) defended the goslings by standing over them with cupped wings. They also defended against conspecifics and Herring Gull attacks. The removal of one of the pair resulted in loud "mate calling" by the other. During a subsequent 10-min period, no male arrived in response to the calling.

Both adults and goslings were collected and sexed by dissection, and either the livers (adults) or carcasses (goslings) were frozen at −20°C, 140 min after collection. DNA was extracted from liver tissue by homogenizing 0.3 g in 1 ml of 10 mM Tris, 10 mM NaCl, 2 mM EDTA, pH 8.0, and processing the homogenate as described for blood-DNA extraction (Quinn and White 1987a). Aliquots of each genomic DNA sample (5 μg) were digested with one of the four restriction enzymes *Hin*dIII, *Taq*I, *Msp*I, and *Eco*RI, electrophoresed on 1% agarose gels, and Southern blotted onto Gene Screen Plus membrane (New England Nuclear) as described elsewhere (Quinn and White 1987a). These blots were hybridized with a number of radioactively labeled DNA probes which were known to detect RFLPs (Quinn and White 1987a).

TABLE 1. Genotypes of female parents and goslings.

Probe	Site	F1	F2	G1	G2	G3	G4	G5	G6	G7
DQSG1	AI-	1,2	2,2	1,2	1,2	1,2	2,2	2,2	2,2	2,3
	AII-	2,2	2,2	2,2	2,2	2,2	2,2	2,2	2,2	2,2
	CI-	1,2	1,1	1,2	1,2	1,2	1,1	1,1	1,1	1,1
DQSG2	DI-	1,1	1,2	1,1	1,1	1,2	1,2	1,2	1,1	1,2
DQSG4	BI-	1,2	1,1	1,1	1,2	1,1	1,1	1,1	1,1	1,1
DQSG5	BI-	1,1	1,1	1,1	1,1	1,1	1,1	1,1	1,1	1,1
	BII-	1,1	1,2	1,1	1,1	1,1	1,2	1,1	1,1	2,2[a]
	BIII-	1,1	1,1	1,1	1,1	1,1	1,1	1,2	1,1	1,1
DQSG6[d]	AI-	1,2	1,2	1,1	1,2	1,2	1,2	1,2	1,1	1,2
	AII-	1,2	1,1	1,2	1,1	1,1	1,1	1,1	1,1	1,1
	AIII-	1,1	1,1	1,1	1,1	1,1	1,1	1,1	1,1	1,2
	BI-	1,2	1,1	1,1	2,2[b]	1,2	1,1	1,2	1,1	1,1
DQSG7	BI-	1,2	2,2	1,1[b]	1,1[b]	1,1[b]	2,2	1,2	1,2	2,2
	BII-	1,2	1,2	1,2	1,2	1,2	2,2	1,2	1,2	1,2
	BIII-	1,1	1,1	1,1	1,1	1,1	1,1	1,2	1,2	1,1
	BIV[c]-	1,1	1,1	1,1	1,1	1,1	1,2	1,1	1,1	1,1
DQSG8	BI-	1,1	1,1	1,1	1,1	1,1	1,1	1,1	1,1	1,1
	BII-	1,1	1,1	1,1	1,2	1,2	1,1	1,1	1,1	1,1
	DI-	1,1	1,1	1,2	1,2	1,2	1,1	1,2	1,1	1,2
	DII-	2,2	1,1	2,2[b]	2,2[b]	2,2[b]	1,1[a]	1,2	1,1[a]	1,2
DQSG10[e]	DI-	1	1	1,1	1,2	1,1	1	2	1,1	1
	DII-	W	W	—	—	—	W	W	—	W
	DIII-	2	2	1,2	1,2	1,2	1	1	1,2	1
DQSG11	DI-	1,1	2,2	1,2	1,2	1,1[b]	1,2	1,2	1,2	1,2
DQSG12	BI-	1,2	1,2	1,1	1,1	1,1	1,2	1,1	1,1	1,1
	CI-	1,1	1,1	1,2	1,2	1,1	1,2	1,1	1,2	1,2
DQSG13	BI-	1,1	1,2	1,1	1,1	1,1	1,2	1,2	1,2	1,1
DQSG15	AI-	1,2	1,1	2,2[b]	2,2[b]	2,2[b]	1,1	1,1	1,1	1,1
	BI-	1,1	1,1	1,2	1,1	1,2	1,1	1,1	1,1	1,1
DQSG16[f]	CII-	1,2	2,2	1,2	1,1[b]	1,1[b]	1,2	2,2	1,2	1,2
DQSG17	AI-	1,1	1,1	1,1	1,1	1,1	1,1	1,1	1,1	1,1

[a] F1 excluded as biological mother.

[b] F2 excluded as biological mother.

[c] Previously undescribed polymorphism; BIV-1 = 4.5 kb; BIV-2 = 5.0 kb.

[d] Redesignated to a site-by-site nomenclature for purposes of this paper (contrary to Quinn and White 1987a) as AI-1: 3.4 kb; AI-2: 2.8 kb; AII-1: 4.4 kb, 6.3 kb; AII-2: 10.7 kb; AIII-1: 4.4 kb; and AIII-2: 7.8 kb.

[e] DI and DIII are polymorphisms on the Z chromosome, hence females are hemizygous. DII is a W homologous band which females carry and males lack (Quinn, Cooke, and White in prep.).

[f] Previously undescribed polymorphism; CII-1: 1.1 kb; CII-2: 0.9 kb.

RESULTS

We determined the genotypes of all birds sampled from autoradiographs of the probed blots. The autoradiograph obtained using the DNA probe DQSG7 is shown and described in Fig. 1. The BI-1 (presence of a 3.7 kb band) and BI-2 (presence of 2.8 and 0.9 kb bands) alleles were particularly informative. The F1 female nest attendant was a heterozygote (1,2) and F2 was homozygous (2,2). Goslings G4 and G7 were homozygous (2,2) and, because both F1 and F2 carry the 2 allele, either could have been their biological mother. Similarly, the heterozygotes (1,2) G5 and G6 could have been parented by either F1 or F2. However, G1, G2, and G3 were homozygous (1,1) and F2 did not carry the 1 allele. Of the two adult nest attendants, F1 was the only possible biological mother of G1, G2, or G3. From data on 30 such genetic markers (Table 1), we concluded that F2 was the only possible biological mother of G4, G6, and G7. G5 remained ambiguous; neither F1 or F2 were excluded as a possible biological parent.

From the relationships between F1, F2, and the goslings (Table 1), we partially reconstructed the genotype of the goslings' fathers at many of these loci. To accomplish this, we obtained higher resolution by considering the alleles at the linked polymorphic sites detected by a single probe as haplotypes. As these probes all span <15 kilobase pairs (kb) of DNA, the probability of a recombination event occurring within one (or several) generations is virtually

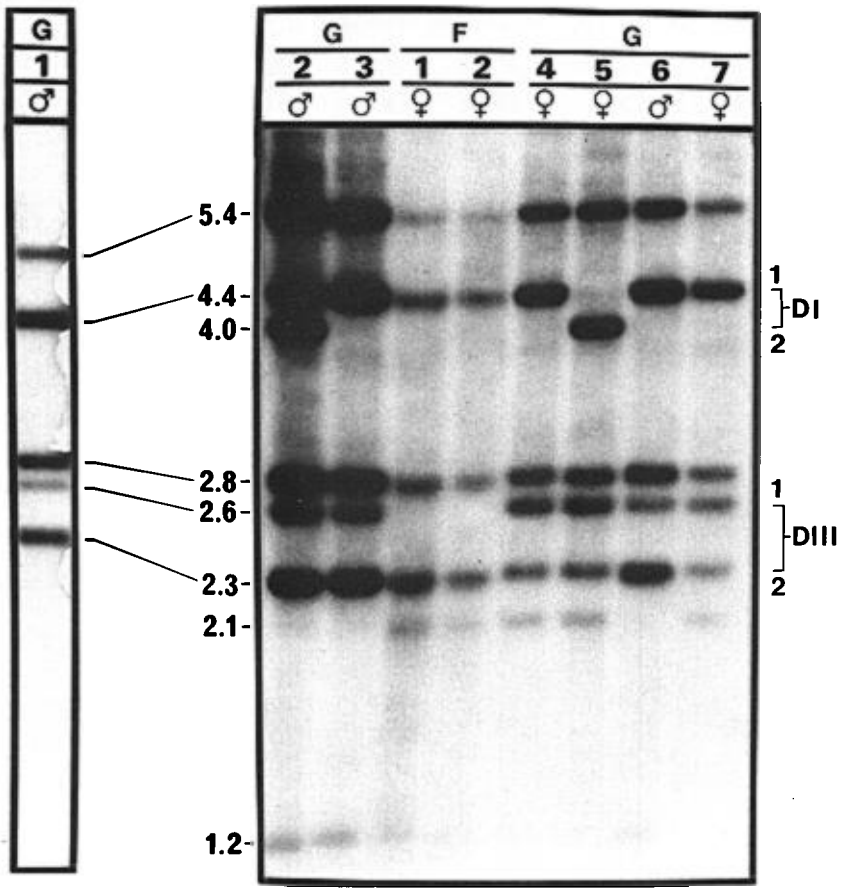

Fig. 2. Autoradiograph showing the detection of sex-linked RFLPs with DQSG10. Samples were prepared as in Fig. 1, except *Taq*I was used along with the probe DQSG10. The 2.1 kb band is W chromosome specific and was present in females only. Polymorphisms at 2 restriction sites on the Z chromosome were detected (shown on right). One (DIII-2) is superimposed on top of a constant 2.3 kb band. G1 was electrophoresed on a different blot; hence the difference in band locations in that lane. Females carry a single allele at each polymorphic site, which directly reflects their paternally inherited Z chromosomal genotype. Males were diploid for the Z chromosome, carrying one paternal and one maternal Z. Because both F1 and F2 carried DI-1 and DIII-2, all male goslings must have inherited these alleles maternally. Thus, the paternal genotypes of the goslings must have been DI-1, DIII-1 (G1); DI-2, DIII-1 (G2); DI-1, DIII-1 (G3); and DI-1, DIII-1 (G6).

nil. We reconstructed the haplotype of a region on the Z chromosome which was detected by DQSG10 (Figs. 2, 3a). In addition to two polymorphic sites on the Z chromosome, DQSG10 detected the presence of a W chromosome (in females) by hybridizing to a 2.1 kb W chromosome-specific DNA fragment (Quinn, Cooke, and White in prep.; Fig. 2). As F1 and F2 were females (2.1 kb band present, sex confirmed by dissection), they were hemizygous, each carrying one Z chromosome. Both carried allele 1 at the DI site and allele 2 at the DIII site, so their haplotypes were represented as 12 (Fig. 3a). The male goslings G1, G2, and G3 each carried a single paternally and a single maternally derived Z chromosome. Because the mother (F1) supplied a 12 haplotype to each, the father must have supplied 11, 21, and 11 haplotypes, respectively. Assuming that G1, G2, and G3 originated from a mating between F1 and a single male, his haplotypes must have been 11/21 (the slash separates the haplotypes on the two homologous Z chromosomes). In the case of female goslings, the haplotype on the Z chromosome came from the father exclusively, as the mother supplied only the W chromosome.

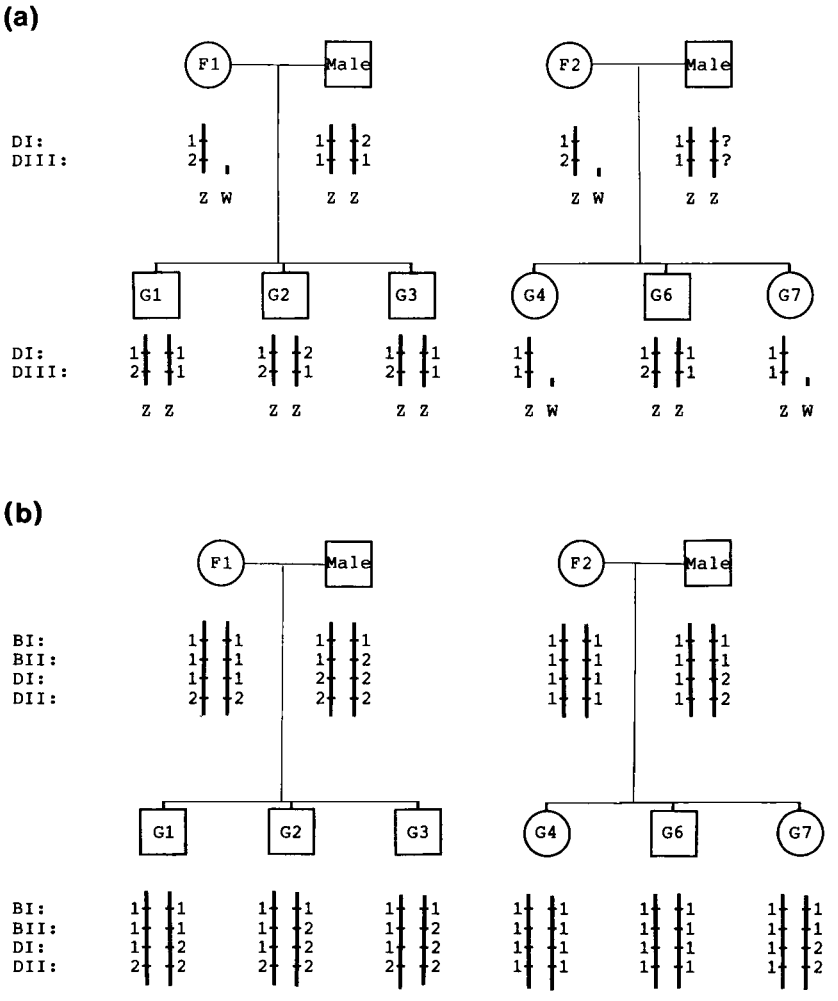

Fig. 3. Paternal haplotype reconstruction at DQSG10 and DQSG8. **(a) DQSG10:** The probe DQSG10 detected 2 polymorphic sites on the Z chromosome. F1 and F2 were hemizygous (female), and each could transmit only the 12 haplotype to male offspring. The other haplotype carried by male offspring, as well as the haplotypes of female offspring, must have been paternally derived. Assuming there was one father for G1, G2, and G3, his haplotypes must have been 11/21. The paternal haplotype of G4, G6, and G7 could be only partially reconstructed because only one paternal haplotype was detected (or because he was 11/11). G5 was not grouped by exclusion with either F1 or F2 and was excluded. Because the reconstructed haplotypes of the 2 male parents were not exclusive, a single male may have fathered all of the goslings. **(b) DQSG8:** F1 and F2 were homozygous at all sites detected by DQSG8 (BI, BII, DI, DII) and could each pass only 1 haplotype to their offspring (1112 and 1111, respectively). The alternate haplotypes carried by their offspring (G1–G7) must have been paternally derived. Taken together, G1–G3 carry both 1122 and 1222 in addition to the (F1) 1112 haplotype. Assuming one father, his haplotypes must have been 1122/1222. The paternal haplotypes of G4, G6, and G7 could also be reconstructed as 1111/1122. Note that the 2 males' reconstructed haplotypes do not correspond.

Hence, the male reconstructed for the F2 mating (Fig. 3a) carried a 11 haplotype. His other Z chromosome could not be determined from this pedigree because G4 and G7 (and G6, following the reasoning of the other male goslings G1–G3) all carried a paternal 11 Z chromosome. The haplotypes of the two reconstructed males were not exclusive of each other, so based on this evidence alone, it is possible that a single male fathered all of the goslings.

TABLE 2. Haplotypes of goslings and female attendants at regions which contain >1 polymorphic restriction site, and the reconstructed haplotypes of fathers. Each female nest attendant (F1 and F2) is grouped with its presumed offspring (see Table 1). Where possible, the paternal haplotype of each grouping has been reconstructed (RM). Symbols (AI . . .) indicate order of polymorphic sites used in haplotype designations.

	Probe		
	DQSG1 AI,AII,CI	DQSG5 BI,BII,BIII	DQSG6 AI,AII,AIII,BI
F1	121/222 or 122/221	111/111	1211/2112[b]
G1	121/222 or 122/221	111/111	1111/1211
G2	121/222 or 122/221	111/111	1112/2112
G3	121/222 or 122/221	111/111	1111/2112[d]
RM[h]	—/—	111/—	1111/1112[c]
F2	221/221	111/121	1111/2111
G4	221/221	111/121	1111/2111
G6	221/221	111/111	1111/1111
G7	221/321	121/121	1111/2121 or 2111/1121
RM[h]	321/221	111/121	1111/(2121 or 1121)[c]
G5	221/221	111/112	1111/2112 or 2111/1112
RM[h]	221/—	—/—	—/—

	DQSG7 BI,BII,BIII,BIV	DQSG8 BI,BII,DI,DII	DQSG10[e] DI,DIII
F1	1111/2211 or 1211/2111	1112/1112	12
G1	1111/1211	1112/1122	11/12
G2	1111/1211	1112/1222[d]	12/21[d]
G3	1111/1211	1112/1222[d]	11/12
RM[h]	1111/—[c] or 1211/—[c]	1122/1222[c]	11/21
F2	2111/2211	1111/1111	12
G4	2211/2212	1111/1111	11
G6	1221/2111[a] or 1121/2211[a]	1111/1111	11/12
G7	2111/2211	1111/1122[d,i]	11
RM[h]	2212/(1221 or 2211)[c]	1111/1122[c]	11/—
G5	1111/2221 or 1211/2121 or 1221/2111 or 1121/2211	1111/1122 or 1112/1121	21
RM[h]	—/—	—/—	21/—

	DQSG12 BI,CI	DQSG15 AI,BI
F1	11/21	11/21
G1	11/12	21/22
G2	11/12	21/21
G3	11/11	21/22
RM[h]	11/12	21/22[c]
F2	11/21	11/11
G4	11/22 or 12/21	11/11
G6	11/12	11/11
G7	11/12	11/11
RM[h]	12/(22 or 12)	11/—[c]
G5	11/11	11/11
RM[h]	11/—[g]	11/—[f]

[a] Two haplotype pairs possible, given haplotypes of the genetic mother.

[b] Assumed haplotypes, given haplotypes of the related goslings (Fig. 4).

[c] Reconstructed haplotypes of the father of G1, G2, and G3 did not have the same haplotypes as the father of G4, G6, and G7.

[d] Assumed haplotypes, given the haplotypes of the genetic mother (Fig. 4).

[e] DQSG10 detects two Z chromosomal polymorphisms (Table 1). Females have only one "allele" (from father); males have two.

[f] Reconstructed haplotypes of the father of G5 did not have the same haplotypes as the father of G1, G2, and G3.

[g] Reconstructed haplotypes of the father of G5 did not have the same haplotypes as the father of G4, G6, and G7.

[h] Reconstructed haplotypes of the fathers. Based on the assumption that F1 is the mother of G1, G2, and G3 and that F2 is the mother of G4, G6, and G7. No assumptions about parentage of G5 made.

[i] F1 excluded as possible parent on the basis of haplotype (only additional exclusions to those of Table 1 are listed).

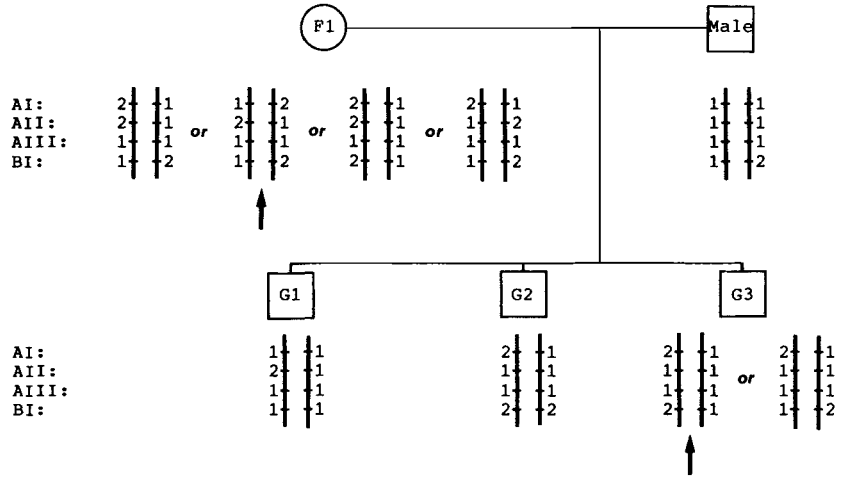

Fig. 4. Paternal haplotype reconstruction at DQSG6. Because F1 was heterozygous at 3 sites (Table 1), she could have had 1 of 4 possible haplotype pairs, depending on the phasing of alleles at the linked sites. As G3 was heterozygous at 2 sites, he could have had 1 of 2 haplotype pairs. If G1, G2, and G3 were offspring of F1, then each should have carried 1 haplotype common to F1. There was only 1 haplotype of F1 and 1 haplotype of G3 which met that criterion (arrow). The male haplotype was reconstructed by the procedure described in Fig. 3b.

A haplotype was reconstructed for the autosomal probe DQSG8 (Fig. 3b). With autosomal probes, females and males carried two alleles. In the example, this was not a problem for phasing the haplotypes carried by F1 and F2, because both were homozygous at all sites, and each could carry (and pass on) only one haplotype (1112 and 1111, respectively). As the reconstructed paternal haplotypes of G4, G6, and G7 did not match the paternal haplotypes of G1, G2, and G3 (Fig. 3b), these data imply that two different males must have been involved in the matings that lead to G1, G2, and G3 vs. G4, G6, and G7. Further genetic support for this conclusion was provided by similar analyses done at DQSG6, DQSG7, and DQSG15 (Table 2).

The third example (Fig. 4) was a case where the haplotype of the female parent (F1) was ambiguous due to heterozygosity at 3 sites. This allowed four possible pairs of haplotypes to be constructed, depending on the phase of alleles at the different linked sites. Also, the alleles of G3 could have been in one of two possible phases, so that unlike the previous cases, the correct pair of haplotypes in G3 could not be determined immediately. It was possible to work backwards to determine the adult female haplotypes. Each gosling presumably inherited one haplotype from F1, and the correct F1 pair of haplotypes must have had a minimum of one haplotype in common with G1, G2, and G3. The only haplotype arrangements satisfying these conditions in the pedigree was 1211/2112 for F1 and 1111/2112 for G3. Following these assignments we reconstructed the male haplotype as 1111/1112.

Although neither F1 nor F2 was ever excluded as a possible genetic parent of G5, it was possible to reconstruct a partial paternal haplotype wherever G5 was homozygous (Table 2). One of these (DQSG12) excluded the reconstructed paternal haplotype of G1, G2, and G3; and another (DQSG15) excluded that of G4, G6, and G7. This implied that a third male was involved with the fertilization of the eggs and was consistent with the idea that G5 was the result of intraspecific brood parasitism or that F1 or F2 was fertilized by more than one male.

Discussion

We used genetic analysis to show that both females contributed to the SNC and that at least three males were involved in the fertilization of those eggs. Evidence that this represents a "true" FF pair and is not a case of polygyny comes from the second point. The analysis was performed in the absence of extensive observational data as would be required in nongenetic studies of FF pairs. We feel that RFLP

analyses are most useful in cases where FF pairs are rare, which makes it impractical to collect adequate observational data, or in cases where determination of parentage is important.

Sexing of attendant parents is another problem often encountered in studies of FF pairs. While this can often be done using morphometric measurements (Ryder 1978), it is difficult for some size groups (Conover and Hunt 1984a) and species. As Conover and Hunt (1984a) have shown that skewed sex ratios in a population may encourage the formation of FF pairs, the sexing of large numbers of birds in a population is also of interest. This can be done using sex chromosome specific DNA probes (Fig. 2, see also Quinn, Cooke, and White in prep.). This precludes the necessity for traditional dissection or laparotomy for sexing (Hunt and Hunt 1977, Conover et al. 1979, Ryder and Somppi 1979, Hunt et al. 1980, Conover 1984).

In many gull species FF pairing appears to be a strategic behavior used by females unable to find stable male partners (Hunt and Hunt 1977; Hunt et al. 1980; Conover and Hunt 1984a, b). The frequency of FF pairs in the Lesser Snow Goose appears to be very low, as an ongoing study of the Snow Goose at La Perouse Bay since 1968 has not detected previously such pairs. At present, there is no evidence to suggest that the male/female ratio is significantly skewed in Snow Goose populations.

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