EVIDENCE OF FORMER ALLOPATRY OF THE TWO COLOR PHASES OF LESSER SNOW GEESE (*CHEN CAERULESCENS CAERULESCENS*)

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ABSTRACT.—Plumage color is distributed clinally in the Gulf Coast population of the dimorphic Lesser Snow Goose (*Chen caerulescens caerulescens*); the white phase predominates in the west, and the blue phase in the east. A similar distribution occurs in the breeding colonies of this population. Historical evidence, stretching back to the mid-18th century, shows that the two phases were almost allopatric until the third decade of the 20th century. Allozyme variants at 6 loci also support the conclusion that the morphs were until recently two distinct taxa. The recent merging of the taxa probably is due to a change in winter feeding habits that allowed birds of both morphs to meet in the rice-growing areas of inland Texas and Louisiana. Because pair formation occurs at this time, this change permitted gene flow to occur between the morphs. There is no evidence of reduced fitness among mixed pairs, and interbreeding among the morphs is common. We know of no other case of a historically documented merging of two formerly allopatric taxa of birds where interbreeding is so widespread and where there is no evidence of reduced fitness of the hybrids. *Received 30 January 1987, accepted 26 February 1988.*

GENETICALLY based plumage polymorphisms occur widely among birds and are present in 25 of 134 families (Huxley 1955). In herons, skuas, and hawks they are relatively common. In other taxa they are present only in one or two species among the group (e.g. geese, wheatears, thrushes, tanagers, oystercatchers, cuckoos, owls). Why the polymorphism should be present in some species and yet absent from closely related species is not known, although several adaptive explanations for polymorphism have been proposed for particular species or groups (Paulson 1973, Arnason 1978).

The genetic basis of plumage polymorphism has been elucidated in only a few cases. The color phases of the Parasitic Jaeger (*Stercorarius parasiticus*) can be explained by a single gene difference, with the dark phase incompletely dominant over the light (O'Donald and Davis 1959). Cooke and Mirsky (1972) showed a similar pattern for the Lesser Snow Goose (*Chen caerulescens caerulescens*) in which the "blue" phase is incompletely dominant over the white phase. Rattray and Cooke (1984) extended this work, ruling out more complex alternative explanations. Several other species (e.g. Variable Oystercatcher, *Haematopus unicolor*, Baker 1973;

Antarctic Giant-Petrel, *Macronectes giganteus*, Shaughnessey 1970; and Ferruginous Hawk, *Buteo regalis*, Schmutz and Schmutz 1981) show segregation patterns similar to those in snow geese, suggesting a single gene difference between the two color phases. This may prove to be the common (but not universal) genetic basis for plumage polymorphism.

Often when a species is polymorphic, the color phases are not randomly distributed but show regional variation in phase ratios. This may appear as a clinal distribution, with one phase predominant in one extreme of the range and another at the other. Examples include the Parasitic Jaeger, Eastern Screech-Owl (*Otus asio*), Common Murre (*Uria aalge*), Northern Fulmar (*Fulmarus glacialis*), and Red-footed Booby (*Sula sula*). Two types of explanation are usually proposed for the nonrandom distribution of color phases. In one it is assumed that differential selection pressures operated in different parts of the range, such that one phase has a selective advantage in one area while the other phase is advantageous elsewhere. To account for the persistence of the polymorphism, some gene flow is essential. Although this seems a biologically satisfactory explanation, we know of no

case in birds where it has been conclusively demonstrated. In fact, in Lesser Snow Geese, where the question has been examined extensively, no selective advantage to either color phase has been found for any measured component of fitness at the predominantly white-phase breeding colony at La Perouse Bay, Manitoba (Cooke et al. 1985, Rockwell et al. 1985).

The second type of explanation assumes that historical accident accounts, in great part, for the distribution. If a mutation for plumage color occurs in one part of the range, it may increase in frequency because of genetic drift, selection, or both. The present-day distribution depends on where the original event, or events, occurred and not on differential selection pressures across the range. Cooch (1963) postulated such an explanation for the breeding distribution of Lesser Snow Geese. Blue-phase birds, which predominate in the Baffin Island colonies, were assumed to have arisen by a favorable mutation that was gradually increasing in frequency throughout the range. Proof of this second type of explanation is very difficult, if not impossible, to obtain because it requires knowledge of past plumage distributions. Because plumage cannot currently be discriminated in fossil material, we must rely on evidence of changes in distribution within recorded history.

The two types of explanation are not mutually exclusive, and differ essentially as to whether selection pressures vary among the color phases across the range of the species. Both explanations assume that the color phases are, and have always been, part of the same potentially interbreeding population. In some ways, the clinal distribution of color phases within a population is similar to the distribution of formerly allopatric taxa that have merged and produced a zone of hybridization. For example, the distribution of Northern Flickers (*Colaptes auratus*) seems to be readily explained by assuming introgression of formerly allopatric populations with extensive hybridization and production of fertile offspring at the zone of contact (Short 1965, Moore and Buchanan 1985, Grudzien et al. 1987). Although western and eastern populations differ primarily by having red or yellow underwings, respectively, the populations also differ in other plumage characteristics. But the hybridization explanation has not been used to explain polymorphisms such as those mentioned above. The reluctance no doubt stems partly from demonstrated or pos-

tulated single gene control of several conspicuous polymorphisms and the notion that allopatric populations should differ at many loci.

Evidence that the plumage dimorphism in the Lesser Snow Goose has arisen through the merging of two formerly allopatric forms came from an investigation of recent phase ratio changes in northern breeding colonies of this species (Geramita et al. 1982). The model used in that study assumed that birds from the various breeding populations in Hudson Bay and Foxe Basin meet in the wintering areas of Texas and Louisiana, where mate selection occurs. When pair formation takes place among individuals from different breeding colonies, the males return to the females' natal colony. The resulting gene flow between the colonies is now massive (up to 50% in small colonies), and one would expect them to equilibrate quickly in terms of phase ratio (Rockwell and Cooke 1977). Despite this, the persistence of phase-ratio differences among the breeding colonies (Cooke et al. 1975) reflects the influence of nonrandom mating and a clinal southern distribution. Mate choice is greatly influenced by family color, leading to partial positive assortment; mixed pairs are only 40% as common as expected under random mating. White birds predominate in the western portion of the southern cline; blue birds are more frequent in the east. These two factors retard but do not prevent eventual equilibration of the phase ratios at the different colonies. Increases in the relative frequency of blue birds at the predominantly white colonies and of white birds at the predominantly blue colonies are expected from the model, and such changes have been observed at some of the breeding colonies. The rate of change in phase ratio is sufficiently rapid to suggest that the two morphs were formerly more isolated from one another than they are today and that the mixing of the morphs could have occurred as recently as 10 generations ago.

Additional evidence suggesting former allopatry relates to the migration of birds from the northern breeding colonies. White birds from all the breeding colonies studied have a more westerly fall migration route and wintering range than blue birds from the same colonies, although separation was far from absolute (Cooch 1961, Lemieux and Heyland 1967, Cooke et al. 1975). One possible explanation is that geese have strong wintering-ground philopatry that may be transmitted from parent to off-

spring. If this is the case, then the tendency of color phases to migrate differentially may reflect a historical pattern, with the original wintering grounds of the blue geese in the eastern part of the range and those of the white geese more westerly.

If indeed the two color phases were formerly allopatric, then two predictions follow. First, because this is a conspicuous polymorphism and is well known to hunter and ornithologist, there should be historical evidence for the postulated changes in distribution of the phases. Second, if the two color phases were recently allopatric, then one might expect other gene and gene-frequency differences between the two populations. These differences could have arisen by drift, selection, or both when the two populations were allopatric, and although the two morphs now interbreed some residual gene-frequency differences between the blue- and white-phase birds are expected. Differences would be strongest in genes linked to the color locus itself, but, even if unlinked, genetic differences in the original populations might still manifest themselves in the present populations because of nonrandom mating.

We document the evidence from these two distinct sources, historical and biochemical, to show that blue geese and snow geese are taxa that have merged only recently.

HISTORICAL EVIDENCE

We examine historical evidence from wintering grounds, breeding grounds and migration routes. All three areas show considerable changes in phase ratio within the twentieth century.

Wintering grounds.—This is the most important area because gene exchange occurs here. Records of the distribution of the two phases have been difficult to obtain in earlier centuries, partly as a result of confusion of plumages. The blue phase was confused with the juvenile plumage of the white phase (e.g. Baird et al. 1858). In addition, the coastal marshes of Texas and Louisiana were often inaccessible. Oberholser (1974) noted frequent 19th-century records in Texas of white-phase geese at locations from the Mexican border in the west to the Louisiana border in the east. For example, J. A. Loring reported flocks of hundreds seen 50 miles (80 km) north of Brownsville on 12 February 1894. H. P. Attwater referred to them as abundant winter residents near Aransas (1891–1894), and several thousand were seen at Anahuac on New Year's Day 1898 by P. R. Litzke. By contrast, blue-goose records for Texas in the 19th century were extremely rare, with only 5 records noted by Oberholser. These refer to birds "taken" by "met with," and there are no suggestions of blue-phase birds in any number.

We have not uncovered any 19th-century records for Louisiana, but in the early years of this century McAtee (1910, 1911) and McIlhenny (1932) reported that the white phase predominated in the extreme southwest corner of the state at Sabine, where blues were rare. Along the rest of the Louisiana coastline, from Vermilion Bay to the Mississippi Delta, blues predominated but a few whites were usually mixed with them. It appears from these early observations that there was a narrow area in southwestern Louisiana (Cameron Parish) were blues and whites overlapped in reasonable numbers. In most of coastal Texas and extreme southwestern Louisiana only whites were found, while blues predominated in the rest of coastal Louisiana. At the time of pair formation most birds had access to potential mates of their own plumage color. Blues probably strayed into Texas less often than whites did into central and eastern Louisiana. McIlhenny (1932) stated that there was about 1 snow goose to every 65 blue geese in the major wintering areas of the blue goose. McAtee (1910) suggested a ratio of 1:25. Both observers stated that snow geese mix with the blue geese rather than forming flocks of their own.

Data on the distribution of the phases are infrequent in the second and third decades of the 20th century but confirm the earlier distribution. Pearson (1922) recorded large numbers of snow geese and one blue goose at Laguna Largo, south of Corpus Christi, on 23 December 1921. A Christmas Bird Count in the same area in December 1921 recorded 35 snows and no blues. The first record of numbers of blue geese in Texas was in 1918. Helmuth (1920) observed 500 from a ship anchored off Sabine Pass, close to the Louisiana border. In the late 1920's large number of the blue birds appear in Texas. Six thousand were reported at the surprisingly western location of Port Lavaca (96°40'W) on 12 January 1929. Five thousand were reported at Port Bolivar. It seems that toward the end of the decade the two color phases were coming more into contact. This continued into the 1930's,

TABLE 1. Christmas Bird Counts of blue and snow geese reported in Texas (TX) and Louisiana (LA), 1930–1945.

Date	Count	Longitude (°W)	Snow	Blue	% blue
26 Dec 1932	New Iberia, LA	92°50′	22	184	89
27 Dec 1932	New Iberia, LA	92°50′ (addendum)	900+	8,000+	90
21 Dec 1938	Aransas, TX	96°50′	157	19	11
? Dec 1938[a]	Cove, TX	94°50′	40	10	20
? Dec 1938	Harlingen, TX	97°20′	575	0	0
15 Dec 1939	Delta, LA	89°20′	8	2,380	99.7
17 Dec 1939	Aransas, TX	96°50′	342	32	9
23 Dec 1940	Delta, LA	89°20′	175	73,000	99.8
24 Dec 1940	Cove, TX	94°50′	60	20	25
26 Dec 1941	Delta, LA	89°20′	14	8,595	99.9
21 Dec 1941	Aransas, TX	96°50′	340	62	15
23 Dec 1942	Sabine, LA	93°30′	670	360	35
26 Dec 1942	Aransas, TX	96°50′	2,100	1	0.5

[a] ? indicates the exact day in December is unknown.

according to Christmas Bird Counts (abstracted from Bird Lore 1897–1940, Audubon Mag. 1941–1946, Audubon Field Notes 1947–1970, and Am. Birds 1971–present). At least 50 snow and blue geese were recorded in 13 counts from 1930 to 1945 (Table 1). By this time both color phases could be found throughout the range except close to the Mexican border. In the major wintering grounds of the blue geese at the delta of the Mississippi, snow geese remained rare.

These data indicate that something happened in the late 1920's or early 1930's that caused the two phases to overlap much more than previously. Stutzenbaker and Bullen (1974) suggested how this might have happened. From the late 1800's to the 1930's, the prairie areas, some 80–144 km inland from the traditional salt-marsh wintering areas of the geese, were gradually converted to rice cultivation. This proved very attractive to the geese, and at present more than

200,000 geese use them as feeding areas. Brazda (in litt.) stated, "Geese first started using the rice fields sporadically in Texas in the early 1930's and in Louisiana shortly after." It seems that the opening up of novel feeding grounds allowed much more mixing and possible pairing of the two color phases.

Evidence from Christmas Bird Counts made regularly since the early 1950's suggests no dramatic changes in phase ratios since that time (Table 2). Two counts in the Corpus Christi area were excluded because they show essentially the same pattern as the Aransas count. There was considerable fluctuation over time but no overall change in the relative distribution of color phases. There is some suggestion that the global frequency of blue-phase birds may have increased in the early 1970's and declined thereafter, and a hint that blues may be increasing at the most southwesterly count at Laguna Atos-

TABLE 2. Phase ratios (percentage of blue birds) from Texas (TX) and Louisiana (LA) Christmas Bird Counts. Values are 5-yr averages.

| Count	Latitude (°N)	Longitude (°W)	1950–1954	1955–1959	1960–1964	1965–1969	1970–1974	1975–1979	1980–1985	Global
Delta, LA	29°20′	89°20′	—	(100)	92	96	(100)	—	—	97
Lafayette, LA	30°12′	92°06′	—	—	—	90	—	56	93	83
Sabine, LA	29°50′	93°30′	63	74	66	(87)	67	53	62	66
Johnson Bayou, LA	29°48′	93°40′	—	—	—	—	—	45	48	47
Galveston Bolivar, TX	29°30′	94°30′	(9)	—	18	31	32	19	18	23
Old River, TX	29°50′	94°40′	—	—	—	36	40	33	20	33
Houston, TX	29°45′	94°57′	32	25	44	21	57	23	26	34
Freeport, TX	29°00′	95°21′	—	23	22	27	15	19	19	21
Attwater, TX	29°40′	96°20′	—	—	4	—	—	12	12	11
Aransas, TX	28°10′	96°50′	9	7	9	5	8	6	4	7
Padre Is., TX	27°20′	97°20′	—	—	—	11	6	9	8	9
Laguna Atascosa, TX	26°10′	97°20′	7	10	10	7	5	15	22	10
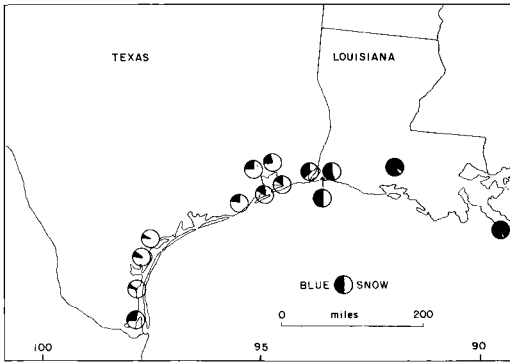
Fig. 1. Phase ratios of Lesser Snow Geese on the wintering grounds. Data are from Christmas Bird Counts, 1979–1984.

TABLE 3. Percentage frequency of blue-phase birds from eastern Louisiana (LA) to central Texas (TX) in 1966. Data are from Lynch (1970).

Location[a]	Latitude (°N)	Longitude (°W)	% blue
Delta NWR, LA	29°20′	89°20′	94.2
Rainey NWR, LA	29°38′	92°12′	92.9
Rockefeller NWR, LA	29°38′	92°36′	91.5
Gueydan, LA	30°01′	92°30′	90.3
Klondike, LA	30°00′	92°35′	84.6
Lacassine NWR, LA	30°00′	92°51′	83.2
Sabine NWR (E), LA	29°51′	93°12′	81.5
Chalkley, LA	29°55′	91°58′	80.3
Gum Cove, LA	30°11′	93°33′	73.5
Sabine NWR (W), LA	29°55′	93°31′	53.6
White Ranch, TX	29°48′	94°23′	52.9
High Is., TX	29°34′	94°24′	40.4
Lissie, TX	29°33′	96°13′	26.9

[a] NWR = National Wildlife Refuge.

cosa. Furthermore, blue-phase birds are relatively more frequent on the inland rice-growing areas of Texas (Old River and Houston) than at equivalent longitudes on the coast (Galveston and Freeport). This suggests that geese attracted to the Texas rice-growing areas in the 1930's included blue geese formerly wintering in Louisiana as well as white birds from the Texas coast. This would facilitate mixing of the two color phases.

There are reasons to treat Christmas Bird Count data with caution. The results are collected by different individuals with varying abilities as observers. Certain parts of an area may be covered in one year and missed in another. Weather conditions vary and may lead to problems of identification. For these reasons we did not perform a rigorous statistical analysis of the data. Nevertheless, some stability of blue-phase ratios since 1950 is suggested. Data from Winter Waterfowl Inventories from 1949 to 1976 give no evidence of systematic switches in phase ratio, and Table 3 presents phase ratios for major snow geese wintering areas in Louisiana and Texas as far west as Lissie Prairie in 1966 (Lynch 1970). These show the clinal distribution of the color phases with a relatively rapid change over a short geographic distance within Cameron Parish, Louisiana (Fig. 1). The stepped clinal distribution has blues predominating in the eastern part of the wintering range and whites in the west. At present both phases can be found in reasonable frequency throughout the winter range. This is in marked contrast to the situation between 1890 and 1920, when little mixing of the phases occurred. Documentation of the actual progression of the change

is scanty, and more historical research is needed. It is clear, however, that widespread sympatry of the two color phases has occurred only during the past 40–55 yr; that is only 10–20 snow goose generations.

Breeding distribution.—Bent (1925) reported nesting of white geese from northern Alaska to Hudson Bay (Southampton Island) and Baffin Island, but nesting blue geese were not discovered until 1929 on the west coast of Baffin Island south of the Koukdjuak River (Soper 1930). Although a few nesting snow geese were found at this location, no mixed pairing was reported and all broods were pure. Two years later, Sutton (1931) reported 2% mixed pairs at Southampton Island. By 1940 more mixing of the color phases occurred. Bray (1943) and Manning (1942) recorded both color phases and mixed pairs at several northern colonies.

With time, the frequency of mixing of both phases in breeding colonies increased. Cooch (1961) noted a gradual increase in the frequency of the blue phase in all colonies between 1940 and 1959. Unfortunately, Cooch's data on phase ratios at Baffin Island were collected under less than ideal conditions, and Kerbes (1975), Ross (pers. comm.), and Dupuis (pers. comm.) have shown subsequently that the relative frequency of blue phase was actually declining at the predominantly blue-phase colonies of Baffin Island. Both color phases now occur in all the Hudson Bay breeding colonies (Table 4), the frequency of whites having increased in the predominantly blue colonies and that of blue in the predominantly white colonies.

TABLE 4. Phase ratios at snow goose colonies, 1955–1963, and recent estimates.

Colony	1955–1963			Recent		
	% blue	Year	Source	% blue	Year	Source
Bowsman Bay, Baffin Island	97	1955	Cooch 1963	81	1975	Kerbes 1975
Cape Dominion, Baffin Island	80	1955	Cooch 1963	61	1975	Kerbes 1975
Koukdjuak River, Baffin Island	53	1955	Cooch 1963	41	1975	Kerbes 1975
Cape Henrietta Maria, Ontario	67	1957	Hanson et al. 1972	71	1979	Ross pers. comm.
East Bay, Southampton Is.	35	1955	Cooch 1963	45	1979	Dupuis pers. comm.
				36	1979–1980	Ankney pers. comm.
Boas River, Southampton Is.	33	1961	Cooch 1963	23	1979	Dupuis pers. comm.
				36	1979	Ankney pers. comm.
La Perouse Bay, Manitoba	24	1963	Hanson et al. 1972	28	1985	Cooke et al. 1985
McConnell River, Northwest Territories	17	1961	Cooch 1963	28	1978	Brace pers. comm.
	24	1961	Hanson et al. 1972			
Central Arctic	5	1960	Cooch 1963	15	1976	Kerbes et al. 1983

Migration routes.—The earliest convincing evidence of the separation of the two morphs is provided by Graham (1769). On the western coast of Hudson Bay (present-day Manitoba) more than 99% of the geese were white, whereas on the James Bay coast (present-day Ontario and Quebec) more than 99% were blue. More than 100 years later the situation had not changed (Barnston 1860, Sanders 1917). Sanders recorded that "on the west coast of James Bay, we get almost nothing but white wavies (snow geese) with an occasional blue in the flock, while on the east coast it is just the opposite."

By 1941 changes in this distribution were evident. Lewis and Peters (1941) reported almost as many blue as white geese in autumn at Albany on the west coast of James Bay, but stated that local residents informed them that 20 years previously blue geese were rare and had steadily increased in frequency. By the 1970's the situation had changed even further. Cooch (pers. comm.) reported the frequency of blue phase as 95% at the Ontario-Quebec border, gradually dropping to 40–50% at the Manitoba-Ontario border. This represents a considerable intermixing of the two phases compared with the historical pattern and suggests a major change occurred sometime after 1917.

The available historical data suggest that the two color phases were almost allopatric before 1920, and that mixing of the phases accelerated in the following decade probably as a result of a change in the pattern of winter feeding. As a result of this mixing, pair formation among the two morphs led to an increase in the exchange of phases among different breeding colonies to such an extent that today both phases are found in all the Hudson Bay and Foxe Basin breeding colonies and throughout the Texas and Louisiana winter range.

BIOCHEMICAL EVIDENCE

The historical evidence indicates that two populations of snow geese, one white and one blue, were reproductively isolated until relatively recently. During this period of allopatry, we expect that detectable differences in allelic frequencies evolved between the isolates and that these might still exist despite the homogenizing effects of recent gene flow. We examined the geese at La Perouse Bay using biochemical markers for evidence of differentiation between blue and white morphs.

Samples of 1–2 ml of whole blood were removed from the brachial vein of snow geese during the annual molts in 1981 and 1982 at La Perouse Bay. Samples were kept on ice packs until separated by centrifugation.They were stored at −15°C during transport back to Nottingham, after which they were maintained at −80°C. There was no evidence of any difference between the samples collected in the two years, and data were pooled. A few goslings that were found moribund in the colony in 1981 were collected, and the livers taken for analysis.

The blood and liver samples were prepared for electrophoresis as described by Cole and Parkin (1981), and analyzed as described by Parkin and Cole (1984). Twenty-eight enzymes or proteins were examined in the 27 liver samples. We defined 44 loci (Appendix) of which we can be certain of 41. Twelve of these show variation that is probably genetically based. Six (Est-C, PepD-2, Ada, Gsr, Mpi, Acon) are polymorphic under the 95% rule (Ferguson 1980), while the remainder (Idh-A, Est-A, PepD-1, Sod, Gpi, Gpd) possess only an occasional rare variant. Two of the polymorphic loci (Acon, Est-C) were resolved only in liver tissue and were of little use in population screening, as were Idh-A and Gpd among the rare variant loci. Variants at the Gpi and Sod loci were so few as to be of no use to the population survey. The 550 blood samples were screened for each of the 6 remaining loci (Table 5).

We tested for difference in allozyme frequency between blue and white geese with analysis by *F*-statistics (Wright 1951). The statistic F_{st} "theta" of Cockerham (1969) reflects differentiation between populations (Weir and Cockerham 1984). There was no evidence of linkage disequilibria between any pair of enzyme loci, so the genotype data can be regarded as independent for each enzyme (Table 6). The unbiased overall estimate obtained by jackknifing was 0.00329 (SD = 0.00144). This was tested for departure from zero (Barker et al. 1986) using

$$\text{chi}^2 = \text{theta}^2/\text{var(theta)} = 5.22, P = 0.02.$$

The value of 0.00329 indicates a slight but significant difference in allozyme frequencies between the blue and white geese. Estimates of theta derived from interpopulation comparisons of avian species, but computed in alternative ways, vary between 0.001 to 0.04 (Bar-

rowclough 1983, Corbin 1983). This suggests that the differentiation between blue and white geese is within the range of avian local populations, albeit at the lower end. This might be expected if introgression following recontact between the two isolates had resulted in some mixing of the gene pools.

Differences in allelic frequencies occurred between the color phases at the Ada, Mpi, and PepD-2 loci. Indeed, the commonest allele differed significantly in frequency at the latter two loci (chi² = 3.47, 4.19, and 5.97, respectively).

F-statistics were used to examine differences in the genetic structure of the two sexes and between age classes. We compared adult males with females within colors and found no evidence of difference. For white geese, theta = 0.0013 (SD = 0.0012), and for blues, theta = 0.0039 (SD = 0.0066). This great similarity is not surprising because snow geese form pairs on the wintering grounds, and each subpopulation makes an equal contribution to the gene pool of both sexes.

We pooled data from the two sexes to allow a comparison with the goslings. The color classes were kept separate. There was no evidence of difference between the age groups: theta white = 0.00189 (SD = 0.00439) and theta blue = 0.00028 (SD = 0.00364). This suggests that there is neither selection during growth nor differential return to the natal colony. Unfortunately, sample sizes were sufficiently small that even large selective differentials might not have been detected.

We next tested for evidence of deviations from Hardy-Weinberg expectations. One locus (PepD-1) had allelic frequencies so extreme that rare homozygotes were virtually never to be expected. The remainder all had some rare alleles and were pooled into a single class (Table 7). In most cases, there was a deficiency of heterozygotes compared with Hardy-Weinberg expectation, although this reached significance only for PepD-2 (the significance of Gpi was due to a small number of expecteds in one homozygote). Dividing the PepD-2 data by age, sex, and color showed (Table 8) that significant departures from equilibrium occurred consistently among white birds. The individual probabilities for each age/sex combination were pooled using Fisher's (1954) formula: $\text{chi}^2_n = -2$ ln(*P*) for *n* independent probabilities. This yielded $\text{chi}^2_8 = 27.7$ for white geese and $\text{chi}^2_8 = 10.5$ for blues (*P* < 0.01 and *P* > 0.5, respec-

TABLE 5. Allelic-frequency data at 6 loci related to age, sex, and color of snow geese at La Perouse Bay. Alleles are identified by letters; A is the fastest on starch gel.

Age[a]	Sex[b]	Color[b]	Adenosine deaminase							Glutathione reductase				
			A	B	C	D	E	X	Y	A	B	C	X	Z
A	M	W	59	53	17	4	1	2	2	2	131	1	3	1
A	M	B	39	20	15	1	1	0	2	8	58	0	2	0
A	F	W	56	44	8	2	2	1	1	7	107	0	0	0
A	F	B	38	22	8	2	1	0	1	3	69	4	0	0
J	M	W	127	84	23	3	4	0	7	13	228	0	3	0
J	M	B	142	83	24	1	3	0	5	18	239	0	1	0
J	F	W	109	97	16	8	1	0	7	13	217	1	3	0
J	F	B	93	72	16	5	5	0	3	9	179	3	3	0

Age[a]	Sex[b]	Color[b]	Glucose phosphate isomerase							Mannose phosphate isomerase			
			A	B	C	D	E	X	Z	A	B	C	D
A	M	W	0	0	133	1	1	2	1	12	122	4	0
A	M	B	0	0	66	1	0	1	0	9	55	4	0
A	F	W	4	0	108	1	0	0	1	9	99	2	2
A	F	B	1	0	70	0	1	0	0	6	61	5	0
J	M	W	2	4	239	1	1	1	0	6	231	11	0
J	M	B	1	2	250	4	0	1	0	15	232	10	1
J	F	W	3	3	230	1	0	1	0	6	224	8	0
J	F	B	1	0	188	4	1	0	0	10	176	8	0

Age[a]	Sex[b]	Color[b]	Dipeptidase-2						Dipeptidase-1		
			A	B	C	D	X	Y	A	B	C
A	M	W	3	116	15	0	0	0	0	138	0
A	M	B	1	60	5	0	0	0	1	67	0
A	F	W	6	91	14	0	3	0	1	113	0
A	F	B	4	63	5	0	0	0	0	72	0
J	M	W	26	175	15	0	2	2	2	218	0
J	M	B	11	216	18	1	2	2	0	249	1
J	F	W	14	171	10	0	4	1	2	202	0
J	F	B	10	156	11	0	0	1	1	181	0

[a] A = adult, J = juvenile.
[b] M = male, F = female.
[c] W = white, B = blue.

TABLE 6. Comparison of the blue and white geese at La Perouse Bay. F_{st} was calculated according to the method of Weir and Cockerham (1984).

Locus	F_{st}
Adenosine deaminase	0.002336
Glutathione Reductase	0.000063
Mannose phosphate isomerase	0.003178
Dipeptidase-1	−0.000697
Dipeptidase-2	0.004772
Glucose phosphate isomerase	−0.000052
Mean (see text)	0.00329

tively). The deficiency of heterozygotes at the PepD-2 locus was demonstrable only among white-phase geese.

DISCUSSION

The historical data show that changes in distribution of the color phases have occurred. Unlike most species of birds, geese form pairs during late winter or early spring. A change in distribution at this time could allow exchange of genes between populations of taxa. Before 1920 the white and blue morphs were almost allopatric, with the former in the coastal marshes of Texas and the latter in the coastal marshes of central and eastern Louisiana. The two taxa were essentially isolated from one another for at least 150 years before that, although evidence of this comes from the more northerly part of the range. We concur with Ploeger (1968) that the original separation may have occurred in the late Pleistocene, when much of the present breeding range of the blue and snow geese was uninhabitable.

Why the two taxa remained separate in their winter and migration distribution is unclear. Tradition alone may account for the separation, although the possibility of different ecological preferences between the phases in the coastal marshes cannot be ruled out. Changes in the availability of winter feed, brought about by rice and rye-grass planting inland, is likely to have triggered a distributional change in both taxa and allowed them to meet when pair formation was occurring. Other changes may have assisted this process. Coastal marshes were burned periodically, which would cause suitable feeding areas to be unavailable to them. National Wildlife Refuges were established throughout the United States in the early years of the 20th century, and modified the migration routes of the Lesser Snow Geese.

The unexpected feature of the merging of two taxa is that they interbred so freely. Although there is positive assortative mating (Cooch and Beardmore 1959), there is no indication of reduced reproductive fitness of mixed pairs relative to pure pairs (Findlay et al. 1985). In fact, there is some indication that mixed pairs are superior in some components of fitness. In most historically documented cases where two closely related taxa have merged geographically, there has been either a maintenance of reproductive isolation despite the re-establishment of sympatry (Japanese and White wagtails, *Moticilla grandis* and *alba;* Higuchi and Hirano 1983) or the development of a hybrid zone (examples documented by Barton and Hewitt 1985). We agree that populations showing clinal distribution of gene frequencies with large geographic areas of overlap may be a result of primary selection gradients rather than secondary contact. We have provided historical evidence

TABLE 7. Observed and expected numbers of principal genotypes among snow geese sampled at La Perouse Bay. Parenthetical values are the expectations under Hardy-Weinberg conditions. Alleles are identified by letters; A is the fastest on starch gel. R indicates data pooled for rare alleles.

	AA	AB	BB	CC	AR	BR	CR	RR	χ^2	df	P
Ada	155	261	72		92	70		15	5.19	3	>0.1
	(165)	(236)	(84)		(95)	(68)		(14)			
Gsr			571			86		6	1.11	1	>0.1
			(569)			(89)		(4)			
Mpi			546			108		10	3.23	1	>0.05
			(543)			(116)		(6)			
PepD-2			460			128		28	19.46	1	<0.01
			(446)			(156)		(14)			
Gpi				622			40	3	4.37	1	<0.05
				(620)			(44)	(1)			

TABLE 8. Observed number of principal genotypes at the PepD-2 locus in snow geese, arranged by age, sex, and plumage color.

Age[a]	Sex[b]	Color[c]	BB	BR	RR	χ^2	df	P
A	M	W	52	12	3	3.54	1	0.06
A	M	B	27	6	0	0.33	1	0.57
A	F	W	40	11	6	9.16	1	0.01
A	F	B	29	5	2	4.80	1	0.03
J	M	W	72	31	7	1.97	1	0.16
J	M	B	95	26	3	0.56	1	0.45
J	F	W	77	17	6	9.88	1	0.01
J	F	B	68	20	1	0.12	1	0.73

Results pooling probabilities following Fisher's (1954) method:

White	$\chi^2_8 = 27.7$	$P < 0.01$
Blue	$\chi^2_8 = 10.5$	$P > 0.5$

[a] A = adult, J = juvenile.
[b] M = male, F = female.
[c] W = white, B = blue.

for secondary contact in snow geese and know of no other case where merging has been accompanied by such widespread interbreeding. Other cases of avian plumage polymorphism, where there is a clinal distribution of the phases, may have arisen in a similar way.

If the two taxa were formerly allopatric, the genetic composition of the two taxa may have differed at loci other than the plumage color locus when they merged. We documented marginal differences between the color phases at the Ada, Mpi, and PepD-2 loci, which combine to produce a slight, but significant, overall difference. If there were originally differences in allelic frequency at these loci between the two taxa, we might still expect evidence of it if they had merged as recently as 10–20 generations ago.

Departures of genotypic frequencies from Hardy-Weinberg expectation showing a paucity of heterozygotes could arise from selection against the heterozygote, inbreeding due to small population size, nonrandom mating, or the Wahlund effect. We have no evidence that natural selection is acting at any locus. Inbreeding due to small population size is dismissable because pair formation takes place on the wintering grounds from a population of tens of thousands of birds. This leaves nonrandom mating and the Wahlund effect. Both may play a significant role in determining the genetic structure of snow goose populations. Positive assortative mating occurs with respect to plumage and is based on early learning of the color of parents and sibs (Cooke et al. 1976). Although

this will lead to an excess of color-allele homozygotes among the progeny, it will increase the homozygosity only of enzyme loci that are linked to color locus. We have no evidence of such linkage, and any disequilibria between color and enzyme alleles are empirically too slight for such an explanation to be reasonably tenable.

The Wahlund effect is the more likely explanation for the deficiency of heterozygous enzyme genotypes. This phenomenon occurs when a sample is taken that includes individuals from two or more separate subpopulations, each with different allelic frequencies. There will inevitably be heterozygote deficiencies in the combined sample, and the greater the difference in allelic frequency between the subpopulations, the more striking will be the deficiency (Hedrick 1984).

We have shown that there are differences in allelic frequency between blue and white birds that could stem from divergences during the period of separation. The recontact in the 1920's would lead to the fairly rapid establishment of clines at the loci where allelic frequency differences had evolved during isolation. These clines in enzyme frequency need not correspond exactly to the cline of color phases. The fidelity to wintering grounds, and hence to the site of pair formation, means that the birds nesting at La Perouse Bay come from separate subpopulations, which would couple with genetic difference to produce the observed Wahlund effect. The Wahlund effect is more pronounced among the white-phase birds than the blue. This

may be explained by assuming that there are more white-phase birds at La Perouse Bay that have never had a blue phase in their ancestry than blue-phase birds with no white-phase bird in their ancestry. This is likely if the birds from the more westerly parts of the breeding range formerly comprised only white-phase birds, and blue birds appeared only if mated to white females from La Perouse Bay.

Taxonomists debate whether the color phases should be considered as one or two species. There is overwhelming evidence that the two forms have merged and become a single species with a plumage polymorphism. The Lesser Snow Goose should thus be referred to as *Anser caerulescens caerulescens.* It is equally clear that the earlier taxonomists had no evidence of the fertility of hybrids between blue and snow geese, and, because the two forms were visually distinct and geographically separate, it was logical to consider them distinct species or subspecies. The snow goose is to our knowledge the only historically documented case among birds where two taxa have merged into one, with no evidence of reduced fitness among the hybrids.

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APPENDIX.

Enzyme	E.C. no.	Tissue[a]		No. of loci and type of variation[b]		
		Liver	Blood			
Isocitrate dehydrogenase	1.1.1.42	+ +	−		1R	1M
Esterase	3.1.1.1	+ +	+	1P	1R	
Dipeptidase	3.4.11 or 13*	+ +	+	1P	1R	1M
Adenosine deaminase	3.5.4.4	+ +	+	1P		
Glutathione reductase	1.6.4.2	+	+	1P		
Diaphorase	1.6.2.2	+	−			2M
Mannose phosphate isomerase	5.3.1.8	−	+	1P		
6-phosphogluconate DH	1.1.1.44	+	+			1M
Glucose-6-phosphate DH	1.1.1.49	+	+			1M
Tripeptidase	3.4.11 or 13*	+	−			3M
Aconitase	4.2.1.3	+	−	1P		
Superoxide dismutase	1.15.1.1	+	−		1R	1M
Haemoglobin	—	+	+			3M
Phosphoglucomutase	2.7.5.1	+	−			3M
Adenylate kinase	2.7.4.3	+	−			1M
Glyoxalase	4.4.1.5	+	−			1M
Glucose-phosphate isomerase	5.3.1.9	+	+		1R	
Glycerophosphate DH	1.1.1.8	+	−		1R	
Nucleoside phosphorylase	2.4.2.1	+	−			1M
Glutamate DH	1.4.1.3	+	−			1M
Lactate DH	1.1.1.27	+	+			2M
Malate DH	1.1.1.37	+	+			2M
Guanosine deaminase	3.5.4.3	+	+			1M
Albumin	—	−	+			1M
Transferrin	—	−	+			1M
Glutamate oxalate transaminase	2.6.1.1	+	−			2M
Total				6P	6R	29M

[a] + + = strong, + = weak, − = not visible.
[b] P = polymorphic, R = rare variants only, M = monomorphic.

The National Wildlife Federation and the Department of Fisheries and Wildlife Sciences at Virginia Polytechnic Institute and State University will host the **Southeast Raptor Management Symposium** and **Workshop 14–16 September 1988** in **Blacksburg, Virginia,** at the Donaldson Brown Center for Continuing Education. Symposium workshops will encourage participants to discuss regional issues related to raptors and to develop management recommendations.

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