

## ECOLOGICAL ASPECTS OF THE BLUE-SNOW GOOSE COMPLEX

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THE taxonomic relationship of the Blue Goose (*Chen caerulescens caerulescens*) and the Lesser Snow Goose (*Chen hyperborea hyperborea*) has long created controversy among avian systematists, e.g., Blaauw (1908), Soper (1930), Sutton (1932), Manning (1942), and Manning *et al.* (1956). I believe that the two forms are conspecific and that the species consists of two subspecies: a large form, *Chen caerulescens atlantica*, which has no color phases, and a smaller form, *Chen caerulescens caerulescens*, which is polymorphic and has two clearly defined color phases. The remainder of the discussion is concerned only with the latter race.

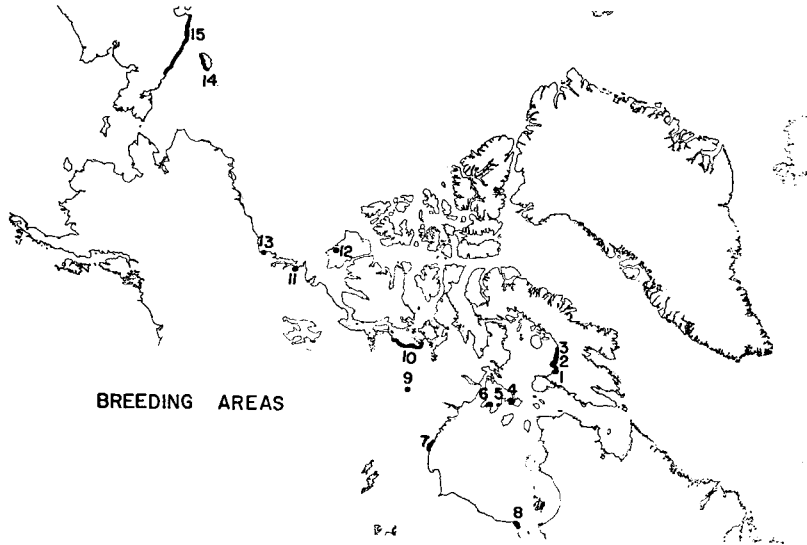
Because of slight pleiotropic differences between the phases, reflected especially in nesting and incubation behavior, some may prefer to follow the lead of Manning *et al.* (1956) and confer subspecific status on *hyperborea*. However, my opinion is that such differences should be considered as dichromatic polymorphs of a single subspecies *Chen c. caerulescens*.

The genetic basis of these color phases is at yet incompletely known and will not be stressed here (cf. Cooch and Beardmore, 1959). Color phases are common among arctic vertebrates and in this case appear to be a form of adaptive polymorphism, which under present climatological conditions gives some selective advantages to blue-phase birds. I shall attempt to define some of the ecological factors influencing the genetic shift toward blue-phase birds.

### DISTRIBUTION

The distribution of the 14 main breeding concentrations is shown in Figure 1. All are located on flat, palaeozoic basins, drained by braided deltas and within five miles of salt water, with the exception of Egg River, Banks Island, which is 16 miles inland (McEwen, 1958).

The percentage of blue-phase birds within any given population is presently greatest at Bowman Bay, Baffin Island, but is increasing rapidly elsewhere, especially within the Hudson Bay drainage. For example, in 1940 the percentages of blue-phase at each colony were as follows: Bowman Bay, 95; Cape Dominion, 50; Koukdjuak, 20; Boas River, 10; Eskimo Point, trace; Perry River, trace. In 1959 the percentages were: Bowman Bay, 97; Cape Dominion, 85; Koukdjuak, 50; East Bay, 35;



**Figure 1.** Location of known major breeding concentrations of *Chen caerulescens caerulescens*. Localities are identified in Table 1.

Boas River, 30; Eskimo Point, 15; Perry River, 9; Banks Island, trace. Evidence of the westward extension of blue genes is the increased number of blue-phase geese reported in migration in recent years from Alberta and California. Details of the recent distributional changes will be presented elsewhere (Cooch, 1960 MS), concomitantly with a discussion of introgression between the phases.

#### PLUMAGE

Plumage color within populations of *Chen c. caerulescens* ranges from white-phase, having six dark primaries and white alulae, to extremely melanistic blue-phase geese. The extent of this variation is most easily detected at colonies such as Boas River, where both phases are relatively common. In white-phase birds, a cline of decreasing frequency of dark alulae can be detected northward and westward from Bowman Bay, similar in nature to the blue to white cline mentioned above. Dark alulae seem to be the first indication of the presence of blue genes in what otherwise would appear to be a pure population of white-phase *caerulescens*.

#### PAIRING

Pairing between phases is common but not random (Cooch and Beardmore, 1959). Progeny from all types of mating are equally viable, and

no difference in egg fertility has been detected. In areas where predominately blue-phase birds have apparently only recently penetrated, adult male heterozygous blues (white-bellied) mated to dark-alulaed white-phase females have pioneered. In most breeding areas where the populations are mixed and blues are in the minority, blue-phase individuals are increasing within those populations at a rate of from 1 to 2 per cent per annum.

#### NESTING

No differences have been detected between the phases with regard to the selection of nesting sites, manner of construction, or defense (Cooch, 1958). Clutch sizes before predation and other loss are identical, averaging 4.42 eggs per complete attempt for both phases under comparable phenological conditions. This is referred to as the theoretical clutch size, since it would occur only in situations where no egg loss occurred.

Since blue- and white-phase birds are differentially affected by varying phenology, the nature of the nest-initiation curves is of utmost importance in analyzing the observed increase of blue-phase birds. *Chen c. caerulescens* constructs nests over a 10-day period, regardless of the phenology of the season, and 12 days after the first nest has been completed and laid in, all laying is terminated. Both phases begin and end their egg-laying activities within the same 12-day interval.

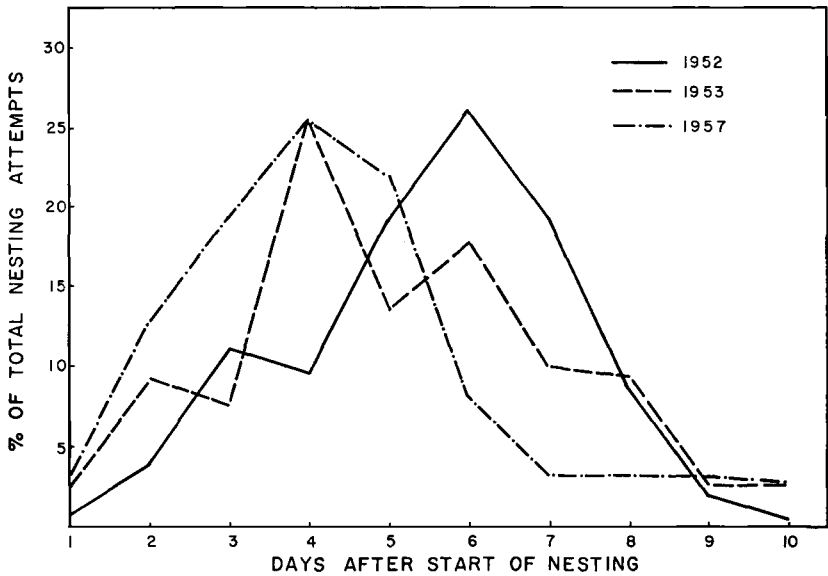
However, the nature of the nesting curve in terms of new nests begun and eggs laid is different for the two phases under differing phenological conditions. Three types of nesting curves are presented in Figure 2, representing early (4-7 June, *e.g.*, 1952), "normal" (8-11 June, *e.g.*, 1953), and late or retarded (12-16 June, *e.g.*, 1957, 1959) seasons. The three curves in Figure 2 are based on all nesting attempts, regardless of phase. The difference between the phases in mean date of nest initiation in retarded seasons is similar to that depicted in Figure 2, if 1957 represents white-phase and 1952 blue-phase nesting attempts. Data in Table 2 indicate that the increase in activity in the first part of a retarded season is clear cut, and the results of such activity will be apparent later in the paper. Throughout the investigation it has been evident that white-phase birds tend to nest earlier than do blue-phase birds except in a very early season (1952).

In itself, this variation is interesting. But its importance lies in the fact that predation and other forms of nesting loss are greatest early in the season and then quickly subside (Cooch, 1956). At Eskimo Point in 1959, 100 per cent of all eggs laid on the first two days of the nest-initiation period were destroyed by Parasitic Jaegers (*Stercorarius parasiticus*) or by flooding. Since white-phase birds tend to nest earlier than

TABLE 1  
SIZE AND POPULATION OF THE MAJOR BREEDING GROUNDS OF *Chen caerulescens caerulescens*

Locality*	Latitude	Longitude	Sq. miles	Population	% blue phase
1 Bowman Bay	65°20' N	73°35' W	250	165,000	97
2 Cape Dominion	65°50' N	74° W	240	100,000	85
3 Koukdjuak	66°20' N	73°55' W	200	75,000	50
4 East Bay	64° 0' N	82°10' W	20	20,000	35
5 Bear Cove	63°40' N	84°45' W	1	1,000	30
6 Boas River	63°42' N	85°45' W	30	25,000	30
7 Eskimo Point	60°30' N	94°50' W	25	15,000	14
8 Cape Henrietta Maria	55°10' N	82°50' W	?	25,000	?
9 Beverly Lake	64°50' N	100°10' W	?	?	?
10 Perry River	67°50' N	102° W	?	?	9
11 Anderson River	69°50' N	129° W	?	5,000	0
12 Egg River	71°50' N	124°50' W	16	20,000	TR
13 Kendall Island	69°10' N	136° W	2	5,000	0
14 Wrangel Island	72° N	180° W	?	?	0
15 Sibertia	70° N	180° W	?	?	0

\* Numbers before localities refer to the position of these localities on Figure 1.



**Figure 2.** Number of nesting attempts started on each day of nest initiation period expressed as a per cent of total attempts—data for both phases are combined.

TABLE 2

VARIATION IN MEAN DATE OF NEST INITIATION MEASURED IN NUMBER OF DAYS AFTER FIRST NESTING ATTEMPT

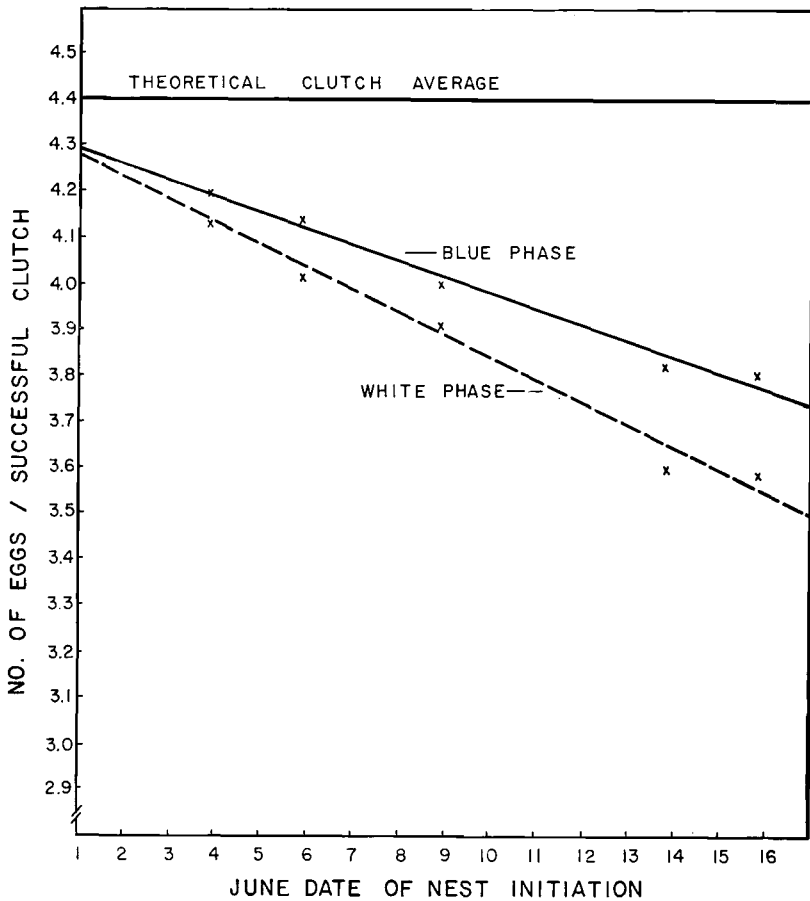
Year	Pair	First nest	No.	Mean	S.D.
1952	SXS	4 June	172	5.5	1.77
1953	SXS	9 June	105	4.0	2.28
1959	SXS	8 June*	238	3.7	1.92
1952	BXB	4 June	65	5.4	1.67
1953	BXB	9 June	11	4.7	1.96
1959	BXB	8 June*	42	4.6	1.83

\* Data for 1952 and 1953 are from Boas River, for 1959, from Eskimo Point. At Eskimo Point 8 June is the phenological equivalent of 12 June at Boas River. Thus, the comparison of years 1952, 1953, and 1959 is effectively a comparison of early, normal, and retarded seasons.

do blue-phase birds, this would suggest that more nests and eggs of the former were destroyed. This does not take into account the number of nests completely destroyed, which increases in the same proportion. However, if a season is extremely retarded (after 14 June at Boas River), a higher proportion of white-phase birds is successful because of an inherent difference in the shape of the nesting curve exhibited by

the phases—during an early season 50 per cent of white-phase and 75 per cent of blue-phase birds nest within two days of the mean date of nest initiation. Complete disruption of a major portion of the nesting pairs would thus affect relatively more blue-phase birds.

Figure 3 shows the effect of retarded seasons on clutch sizes of successful nesting attempts of blue- and white-phase birds. In early seasons the nest-initiation curves are nearly identical, and egg losses are also in the same order of magnitude; but as seasons become more retarded, a higher proportion of eggs from white-phase birds are destroyed.



**Figure 3.** Average number of eggs per successful clutch showing relationship between relative success of blue-phase and white-phase *caerulescens*, and successively later June date of nest initiation.

Figure 4 represents the components of nesting loss in different seasons, based on a sample extrapolated to 1,000 eggs. The net effect of a retarded season appears to be that birds physiologically ready to nest early in the season are prevented from doing so because of weather or snow conditions. However, when extrinsic barriers are removed, competition for available nesting space is intensified, and all those birds still capable of nesting attempt to do so simultaneously. This frequently results in a breakdown of territoriality and leads to desertion and dumping of eggs in other nests, with concomitant decrease in intensity of nest defense. In short, in an early season (4 June) 190/1,000 eggs are

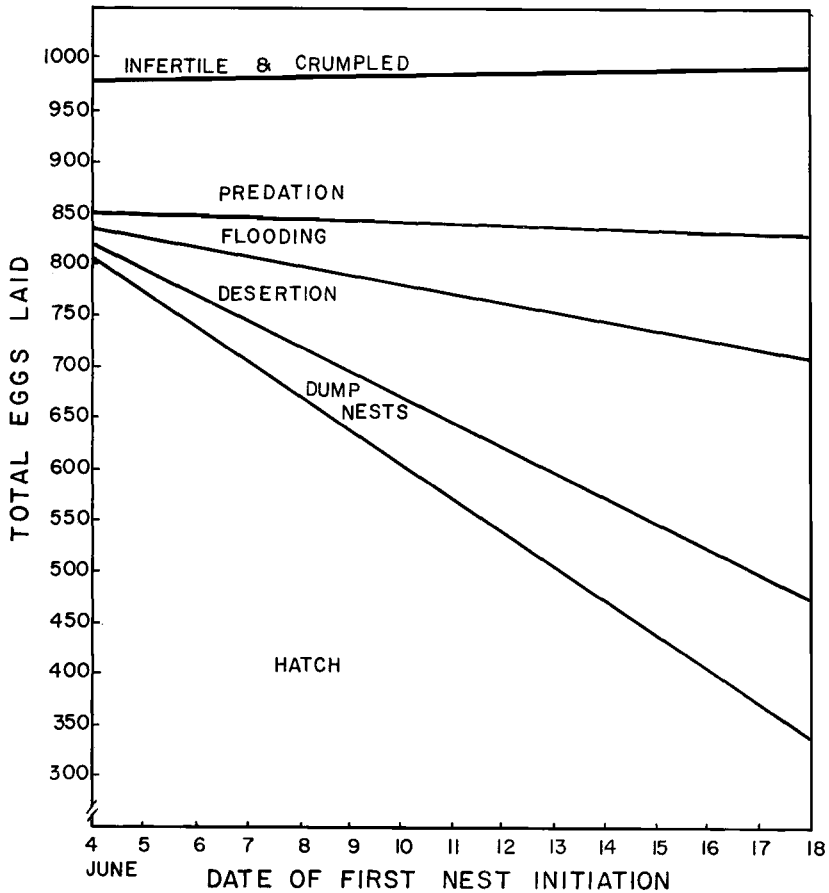


Figure 4. Schematic presentation of components of nesting loss showing variation associated with variation in date of first nest initiation.

destroyed before hatching, in a "normal" season (9 June) 365/1,000, and in a retarded season (13 June) 490/1,000. Complete destruction of a clutch causes the birds to enter their postnuptial molt earlier than do successful breeding pairs. No renesting is attempted, nor can it be induced (Cooch, 1958).

#### CLUTCH SIZES

As stated previously, no difference exists between numbers of eggs laid by the various pairing arrangements (BXB, BXW, WXB, or WXW). Significant differences (6 vs. 3) were found, however, between clutches initiated early in the season and those initiated later. In retarded seasons there is less difference (4.8 vs. 3.0) between early and late clutches. Predation and other forms of nesting loss tend to reduce the difference but never obliterate it. In teleological terms, smaller clutches are "necessary" in retarded seasons or at the end of a normal season in order that reproduction be speeded up. Under optimum conditions, *caerulescens* has 105 days in which to complete its reproductive activities. In a retarded season, the last birds to start laying have only 83 days.

Lack (1947) has postulated several theories on the evolutionary significance of clutch size, based mainly on the premise that, in altricial species, availability of food during brood rearing is a limiting factor. In the case of *caerulescens* and its precocial young, that thesis does not seem to hold. Factors limiting brood size are related to mortality caused by the physical nature of the environment and predation.

Birds laying large clutches do not lay on consecutive days, but after the deposition of the fourth egg, tend to cease laying for two days. As a result nine days are required to lay seven eggs. The most important factor limiting brood size is the phenomenon of interrupted egg laying. Large clutches normally require two days to hatch, but in the event of inclement weather, three or more days may be required. The four eggs that were laid first hatch almost simultaneously. Frequently there is as much as a 96-hour difference in the ages of a seven-gosling brood. As a result, the first hatched are better able to keep up with the adults and do not straggle. The last hatched are weak, tend to straggle, and are unable to compete for brooding space with older members of the brood. The prognosis of survival for such goslings is poor.

There are some data based on serially marked eggs that strongly suggest that, in mixed pairing, white-phase progeny tend to hatch later in any given brood, and are therefore weaker and more susceptible to predation. These data are presented in Table 3. The observed decrease



in frequency of white-phase young in mixed broods as the season progresses is presented in Table 4. The decrease noted in the 10th week after hatching is partly attributable to selective hunting pressure south of the breeding grounds. Few mixed broods larger than four contain any white-phase young after the 10th week.

TABLE 3  
RELATIVE PROPORTION OF WHITE-PHASE GOSLINGS HATCHING IN 64 SERIALLY  
MARKED, MIXED-CLUTCHES, BOAS RIVER, 1952, 1953  
*Egg sequence*

<i>Clutch size</i>	<i>N</i>	<i>1</i>		<i>2</i>		<i>3</i>		<i>4</i>		<i>5</i>		% <i>W</i>
		<i>B</i>	<i>W</i>	<i>B</i>	<i>W</i>	<i>B</i>	<i>W</i>	<i>B</i>	<i>W</i>	<i>B</i>	<i>W</i>	
2	9	9	0	7	2							11.1
3	16	16	0	13	3	10	6					18.7
4	21	20	1	17	4	13	8	10	11			28.3
5	18	17	1	15	3	12	6	10	8	8	10	31.1
Total	64	62	2	52	12	35	20	20	19	8	10	26.2
% White			3.1		18.7		36.3		48.7		55.5	

B = Blue-phase gosling.  
W = White-phase gosling.

TABLE 4  
CHANGES IN PHASE COMPOSITION OF MIXED BROODS FROM TIME OF HATCHING  
UNTIL 12 WEEKS AFTER HATCHING, 1952

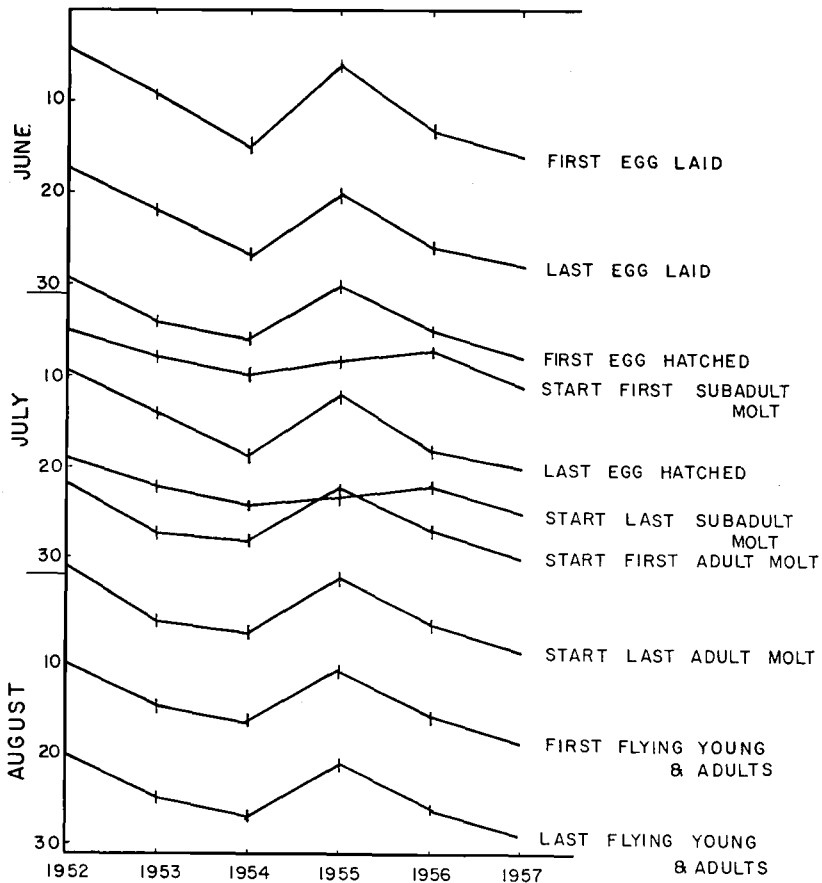
<i>Time</i>	<i>Brood size</i>									Average	% White
	1	2	3	4	5	6	7	8			
Hatch	0	1	3	16	12	1	0	0		4.22	25.5
First week	4	4	6	11	7	2	0	0		3.55	17.9
Tenth week	4	12	8	8	6	1	1	1		3.23	12.5
Twelfth week	3	8	8	6	5	2	0	0		3.33	11.3

The reduction in white-phase goslings in mixed broods is apparently one mechanism by which the percentage of blue-phase birds is increasing. The reverse occurs when both birds of a pair are white-phase geese having dark alulae and laying more than five eggs. In 54 cases observed at Boas River in 1952 and 1953, the last egg laid produced an atypical blue-phase gosling, which eventually became an extreme white-bellied blue-phase adult. The ability of such a gosling to survive the critical posthatch period is slight, and few if any blue goslings are produced by such pairs. Such cases are uncommon except where both phases are relatively abundant.

AUTUMN MIGRATION

The direct differential effect of varying phenological conditions on nest initiation and reproductive success is one basic cause of the observed increase in the proportion of blue-phase birds. The date of nest initiation also affects autumn migration and produces predictable changes from the "norm" (Cooch, 1955), which may bear more heavily on one phase than the other.

Figure 5 shows the relationship between date of nest initiation and all other phenological events. Band recoveries indicate that in early breed-



**Figure 5. Chronology of phenological events 1952-1957 showing the relationship between date of first egg laying and all other events happening on the breeding grounds.**

ing seasons individuals of *Chen caerulescens* breeding at Boas River make a nonstop flight from Hudson Bay to Gulf of Mexico. However, when seasons are retarded, a higher percentage of the population interrupts its migration in the midwestern United States. These data are given in Table 5, where recoveries of adult banded birds from northern states are expressed as a percentage of the total adult recoveries from the United States. In moderately retarded seasons, the rate of recovery for white-phase birds is greater than for blue-phase birds. In extremely retarded seasons, relatively more blue-phase birds are taken. This is apparently a result of the pattern of nest initiation: a high percentage of white-phase birds are geese that have failed to produce young that molt early, and that behave as subadults, *i.e.*, make a nonstop flight to the Gulf Coast. Because blue-phase birds nest a little later, some at least are always successful, but since they are retarded by phenological events, their migration is severely interrupted. Following a phenologically early season, approximately 25 per cent of the total population is removed by hunting pressure; but in retarded seasons, the kill increases to nearly 35 per cent, with most of the increment made up of birds shot in the midwestern United States. Because blue-phase birds are in the minority, but are increasing, adult cohorts contain fewer blue-phase birds than do younger cohorts. The increased attrition on breeding adults would speed up the process of eliminating white-phase birds even if hunting pressure were exerted randomly. Since 1952, 33 bands per hundred from white-phase adults have been returned for each 21 per hundred blue-phase bands. It has previously been shown that in the case of juveniles (which contain the highest proportion of blue-phase birds) white-phase goslings are selected against, both by natural and by hunting predation. This is an example of how man can influence the selection of a color phase by hunting pressure alone without changing the ecological aspect of the breeding habitat.

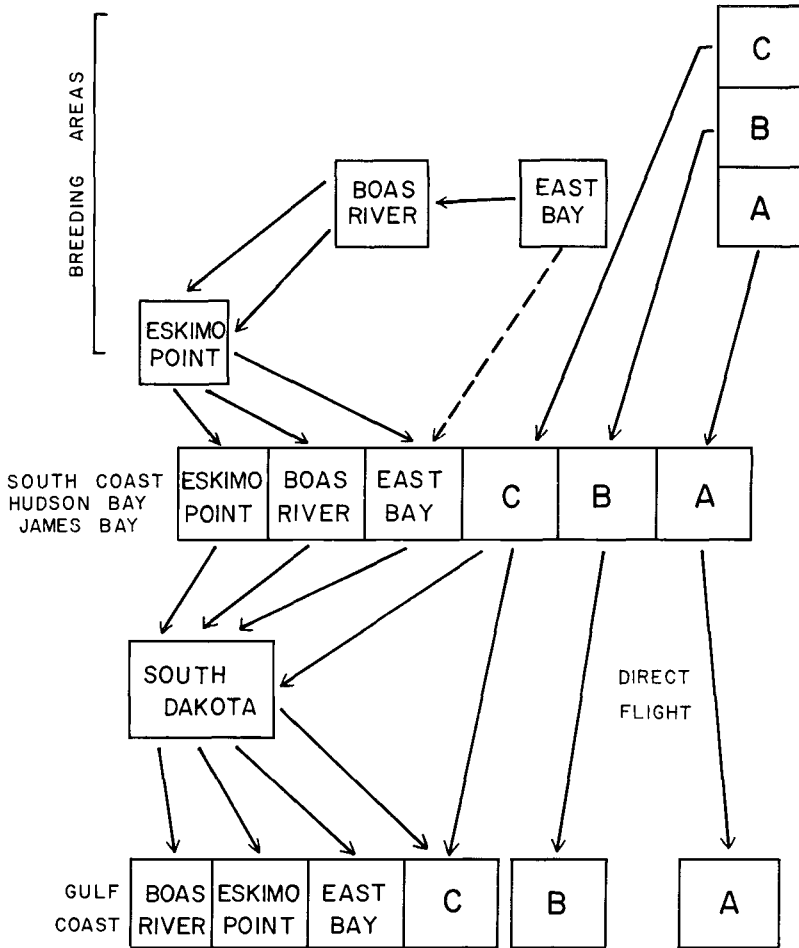
Another factor that influences the spread of blue genes is the distribution pattern of *caerulescens* during breeding, migration, and wintering. Perhaps the most important point is the behavior of the two phases during migration. Five primary aspects of migration apparently affect the recently observed shifts in the frequency of the blue genes. These are:

1. The relatively distinct routes used by the various populations (Figure 6).
2. The observed tendency of blue-phase birds during migration to filter eastward and white-phase birds to filter westward within the bounds of the population flyway.

TABLE 5  
VARIATIONS IN THE NUMBER OF BANDS FROM ADULT BLUE-PHASE AND WHITE-PHASE GEESE  
RETURNED FROM THE UNITED STATES, 1952-1958

Year	Date* June	Northern United States						Southern United States					
		Blue		White		Combined		Blue		White		Combined	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1952	4	0	00.0	2	11.0	2	5.0	22	100	16	90	38	95
1953	9	10	26.3	41	43.6	51	38.6	28	73.7	53	56.4	81	61.4
1954	14	30	66.6	85	59.0	115	60.8	15	33.3	59	41.0	74	39.2
1955	6	4	12.0	13	19.4	17	17.0	29	88.0	54	80.5	33	83.0
1956	12	19	65.5	46	55.3	65	58.0	10	34.5	37	44.7	47	42.0
1957	16	8	47.0	36	57	44	55.0	9	53.0	27	43.0	36	45.0
1958	12	12	50.0	74	69	86	65.5	12	50.0	33	31.0	45	34.4

\* Date of first nest initiation.



**Figure 6.** A schematic presentation of migratory and wintering distribution of six populations of *Chen c. caerulescens* from the Hudson Bay drainage. A = Bowman Bay; B = Cape Dominion; C = Koukdjuak.

3. The tendency of blue-phase birds to make a nonstop flight from James Bay and Hudson Bay to the Gulf of Mexico more frequently than white-phase birds.
4. A greater hunter preference for white-phase birds.
5. Differences in migratory pattern associated with age, breeding success, and phenology.

The first two factors are isolating mechanisms that impede the rapid exchange of genes from one population to another, while the last three factors tend to contribute to selection pressure.

The cline of increasing blue and decreasing white to the north and to the west of Bowman Bay is difficult to explain unless migration by breeding population is considered. Apparently, predominately blue-phase geese have appeared only recently (possibly within the past 50 years) outside of the Baffin Island breeding areas. Salomonsen (1954) has summarized the various types of gene flow, showing lucidly how barriers to the spread of a particular gene need not necessarily be physical, spatial, or behavioral. In the case of *Chen c. caerulescens*, the spread of blue genes was impeded by the intrusion of other populations from Baffin Island, between Bowman Bay, and the breeding and wintering populations from Southampton Island and mainland colonies to the west (Figure 6). Before blue genes from Baffin Island were able to reach Southampton Island, they had to work their way north along the Foxe Basin coast of Baffin Island. This process required not a single generation, but gene movement through a number of generations of geese. This was possible only with an amelioration in climate such as witnessed in the past 50 years. In arctic Canada, this amelioration is mostly found east of a line that runs roughly parallel to the west coast of Hudson Bay (cf. Hare, 1955; Ahlmann, 1955; Willett, 1950; and Lysgaard, 1950). Although both phases begin and end their nesting activity in the same 12-day period, the relative success of white-phase birds in extremely retarded seasons would imply that northward extension of blue genes was inhibited until climatic amelioration occurred. In addition, white-phase birds have a shorter incubation period (23.1 days vs. 23.6 days) than do blue-phase birds, and in regions where the length of the breeding season is reduced, this difference would confer an additional advantage to white-phase birds. The more northerly distribution of white-phase birds presently in existence might be taken as an indication that they are still better adapted for a rigorous environment.

Because geese have strong familial ties and during the first year at least these familial ties remain intact, there is reduced opportunity for new genes to be introduced into any population by the progeny from any given breeding season. Adults that have previously nested in a given area return to that area to breed in successive years (Cooch, 1958). If the parents survive, their progeny also return, at least in their second year. Since *caerulescens* require two and possibly three years to reach sexual maturity, only those three-year-old individuals that have just reached breeding age or those two-year-old birds that have lost their parents are

likely to wander to new areas. Such action by three-year-olds is, however, unlikely, since, during their first summer on the breeding grounds, subadults remain with their parents until the first stages of incubation, then molt on the periphery of the breeding colony. There they associate with second-year and failed-breeding adults. That cohort of the population migrates in mid-August and reaches the wintering areas in early October. Band recoveries from subadults have the same distributional pattern as those from adults and young banded at the same colony. In nearly all extracolony shifting recorded to date (149/184), birds banded as locals have been involved. This is especially true in shifting between Eskimo Point and Perry River (7/7). Whether the shift occurred when the birds were subadults or of breeding age is not known. Band recoveries from the breeding grounds indicate that fewer than one band in 1,000 will be recovered from an area other than that where it was originally attached. This would indicate that each breeding population is relatively discrete. A larger gene flow can be expected from a continuous colony such as exists along the Foxe Basin coast. However, populations or segments of populations tend to resist movement from one locus into other loci.

Because of this conservatism, the Cape Dominion and Koukdjuak populations acted as a barrier to the spread of blue genes to Southampton Island until frequency of the genes in those populations had reached a level whereby a relatively high proportion of heterozygotes was available for emigration. It will be noted that the Koukdjuak population in winter is only partially allohemic with regard to the East Bay and Southampton Island populations. Once blue-phase birds reached the northern limit of the Baffin Island breeding area in numbers, they were then able to drift over into the East Bay population through association during migration and on the wintering grounds. Once that was accomplished, a major barrier to the spread of blue genes had been overcome.

A second factor that tends to act as an isolating mechanism for blue genes may be described as an observed tendency for like to attract like, especially during migration. This is also of importance on the breeding grounds and would have delayed the northward spread of blue genes on Baffin Island into regions of white abundance. It has been observed at Eskimo Point, Perry River, and Banks Island, that the first blue-phase individuals to colonize a new area are white-bellied blue-phase males mated to white-phase females (mostly with dark alulae). The latter are probably the true pioneers, but being predominately white-phase would not generally be detectable. All known westward shifting from Eskimo Point to Perry River has involved white-phase birds whose alulae color

is unknown. As pointed out previously, a pair of dark alulaed white-phase birds having a large clutch (more than 4) are capable of producing an extreme white-bellied blue-phase gosling. It is thus within the realm of possibility that the heterozygotes involved in pioneering have actually been products of this pairing arrangement. This fact in no way changes previous arguments that the frequency of blue genes had to be relatively great before successful emigration could occur.

The fact that like tend to attract like has been clearly demonstrated in band recoveries from the Boas River population. In 1952 and 1953, a total of 13,400 geese were banded there in the ratio of 1 blue-phase to 2.4 white-phase. These birds migrate first to the south coast of Hudson Bay and are hunted from York Factory, Manitoba, eastward to Cape Henrietta Maria, Ontario; few are taken within James Bay proper. As one proceeds east from York Factory, the ratio steadily decreases from 1:2.4 to 1:2.1 at Severn, to 1:1.8 at Winisk, and 1:1 in James Bay. During migration through the United States, recoveries east of the Mississippi are in the ratio of 1:0.8 blue to white, and west of the Mississippi, the ratio is 1:4.0 blue to white. Along the wintering grounds, ratios change from 1:0.5 blue to white at the mouth of the Mississippi River, to 1:2.4 in east Texas, to 1:9.0 in Cameron County, Texas. The greatest rate of band return comes from east Texas, where birds are taken in the same ratio as they occur in the banded population. Segregation on the wintering grounds is important because coastal marshes of Louisiana are relatively less accessible than those of Texas. Blue-phase geese that tend to filter east therefore receive less hunting pressure than do white-phase birds that filter west along the Texas coast. As a result, white-phase birds again tend to be removed from the population at a faster rate than do the blue-phase birds.

#### ACKNOWLEDGMENTS

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## SUMMARY

Blue Geese (*Chen c. caerulescens*) breed in 14 major concentrations from Baffin Island to Siberia. Blue Geese and Lesser Snow Geese (*Chen h. hyperborea*) are considered to be conspecific and color phases of *Chen c. caerulescens*. The center of blue-phase abundance is at Bowman Bay, Baffin Island, but the frequency of blue genes is increasing rapidly, especially in the Hudson Bay drainage. This increase is considered to be an example of adaptive polymorphism, which under present conditions favors blue-phase birds. Mixed pairing occurs but is not random. Progeny from mixed pairs are predominately blue-phase and follow Mendelian segregation. Selection pressure in mixed broods is greatest against white-phase goslings, but equal in pure broods of either phase.

No behavioral differences are noted between the phases, but there are slight differences in the nature of the nesting curve, which in some seasons selects against white-phase birds. Basic clutch size is 4.42, but the number of eggs surviving to hatching time is dependent upon the phenology of the season. A factor limiting brood size is interrupted egg laying and resulting differences in age of goslings within the brood. Since, in mixed clutches, the white-phase tend to be laid last, they are the last hatched and thus less likely to survive. Both phases are more successful in early breeding seasons than in retarded ones, but blue-phase birds and mixed pairs are more successful than white-phase birds, except in extremely retarded seasons. Populations breed, migrate, and winter as discrete entities with little gene exchange. White-phase birds are more likely to exhibit an interrupted migration and are therefore more frequently available to hunters in the United States.

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