

WINTER RANGE EXPANSION AND RELATIONSHIPS BETWEEN LANDSCAPE AND MORPHOMETRICS OF MIDCONTINENT LESSER SNOW GEESE

RAY T. ALISAUSKAS¹

Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada

ABSTRACT.—Dramatic increases in population size and major extensions of winter range have occurred among midcontinent Lesser Snow Geese (*Chen caerulescens caerulescens*) in the last few decades. Agricultural landscapes within these range extensions provide winter foods that are distinctly different from those upon which most birds in this population subsisted until about 1970. I examined geographic variation in body and bill morphology of Lesser Snow Geese by comparing geese from: (1) traditionally used coastal brackish marshes contiguous to the Gulf of Mexico ($n = 314$), (2) agricultural landscapes centered around rice production and occurring up to 160 km inland from the coast ($n = 200$), and (3) agricultural landscapes with extensive corn production about 1,000 km north of the Gulf of Mexico ($n = 125$). Analyses of size and shape in body, head, and bill morphology were done on principal components of 10 metric variables. Geese from marsh habitats were largest in body size, those from rice prairies were intermediate but most variable, and those from the Missouri River valley farthest north were smallest. In addition, “marsh” geese had thicker bills, longer skulls, and longer culmens than “corn” geese. Five nonexclusive hypotheses (phenotypic selection, habitat selection, nutrition, fall migration endurance, and introgressive hybridization with Ross’ Geese [*Chen rossii*]) are proposed to account for this geographic variation in external morphology. The interplay between winter range extension, habitat use, and morphology may have motivated large increases in continental population size and may be coupled with patterns of demographic and morphological change reported on breeding areas. Received 8 September 1997, accepted 1 December 1997.

DOCUMENTED EXTENSIONS OF GEOGRAPHIC RANGE can represent a valuable opportunity for understanding ecological variability and evolutionary dynamics when studied in conjunction with morphological variation. For example, the assumption that geographic variation represents a discontinuity in local adaptations has been used to support much of the evolutionary theory dealing with speciation (Gould and Johnson 1972). However, this assumption has been challenged because such variation can result from environmental induction (James 1983, Zink 1989). At the very least, studies of geographic variation may shed light on ecological variation within different strata of morphologically substructured populations, and perhaps allow quantification of phenotypic change. Moreover, such studies may represent a valuable first step toward understanding the potential for adaptation, or demonstrate evi-

dence of evolution if supported with corresponding genetic evidence.

The relatively recent winter range expansion by midcontinent Lesser Snow Geese from their formerly restricted range is well documented (McIlhenny 1932, Bellrose 1976, Hobaugh 1984, Alisauskas 1988, Bateman et al. 1988) and provides a unique opportunity to study geographic variation in morphology of geese. Initially, this population was confined to brackish marshes along the Gulf of Mexico, roughly from Mexico to the Mississippi River, and was rarely observed more than about 13 km from the coasts of Texas or Louisiana from October to March (McIlhenny 1932; see Fig. 1). Current winter habitat that historically did not harbor Lesser Snow Geese includes former tall-grass prairies found contiguous to marshes along the Gulf of Mexico in Texas and Louisiana; these former prairies (hereafter called “rice prairies” or “rice habitats”) support intensive rice agriculture (Escurieux 1973, Hobaugh 1984) and have been used by wintering Snow Geese only since the late 1950s (Bateman et al. 1988). Winter range at higher latitudes in Iowa, Missouri,

¹ Present address: Prairie and Northern Wildlife Research Centre, Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada. E-mail: ray.alisauskas@ec.gc.ca

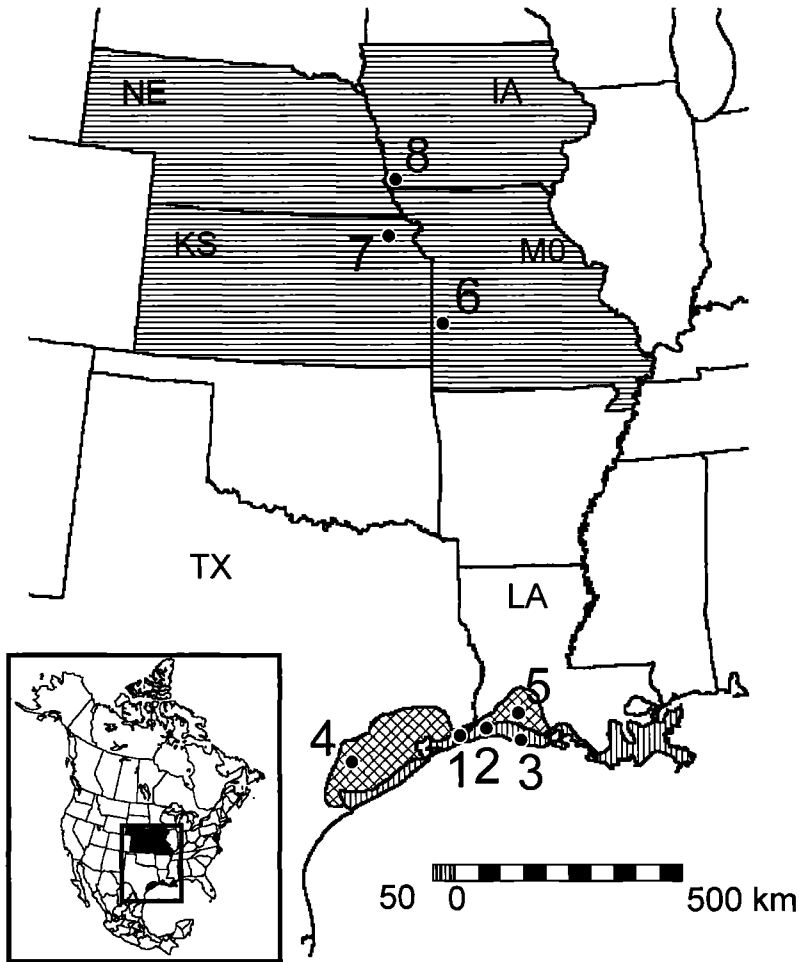


FIG. 1. Locations of Lesser Snow Goose collections during January and February, 1983 to 1984. 1. J. D. Murphree Wildlife Management Area, Texas; 2. Sabine National Wildlife Refuge, Louisiana; 3. Rockefeller State Wildlife Refuge, Louisiana; 4. Garwood Prairie, Texas; 5. Lacassine Prairie, Texas; 6. Schell City, Missouri; 7. Boyle, Kansas; 8. Riverton, Iowa.

and Kansas, includes large acreages of corn, winter wheat, and soybeans (Frederick and Klaas 1982, Davis et al. 1989). The population began to increase in 1970 (Fig. 2) from average winter numbers of 0.7 million during the 1950s, to about 1.6 million by the early 1980s, and 2.7 million in 1994. The start of population growth coincided with the beginning of regular overwintering of Snow Geese at higher latitudes of the midcontinent (Bellrose 1976) and with growing use of rice prairies (Bateman et al. 1988). These events suggest that: (1) the size of the midcontinent population previously may have been limited by winter mortality (see Fretwell 1972) before the 1970s, and (2) the pop-

ulation increase may have resulted from increased overwinter survival associated with expansion of winter range into areas of large-scale agriculture (Boyd et al. 1982).

In these new habitats, Snow Geese are exposed to completely different arrays of foods that differ from their former foods in nutritive quality, structure, and availability (Alisauskas et al. 1988). About 80% of the diet of Lesser Snow Geese that winter in coastal marshes required excavation before consumption; conversely, more than 80% of the food of geese wintering in rice prairies was composed of green vegetation, and more than 80% of the food of geese wintering at higher latitudes was

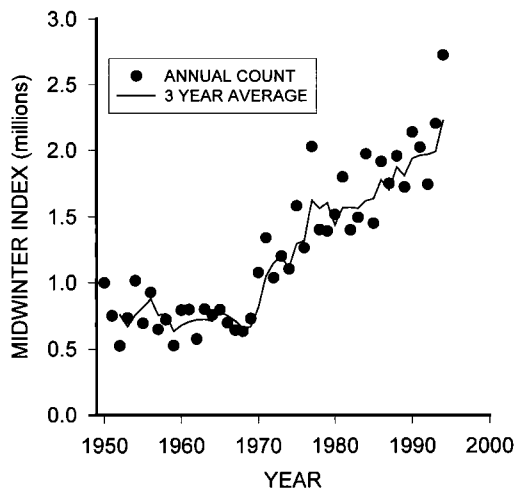


FIG. 2. Time series of midcontinent Lesser Snow Geese counted concurrently in Texas, Oklahoma, Kansas, Nebraska, Iowa, Missouri, Arkansas, and Louisiana during December or the following month, 1950 to 1993. Data compiled from Dzubin et al. (1975), Boyd et al. (1982) and USFWS (unpubl. data).

corn grain (Alisauskas et al. 1988). Thus, Snow Geese that wintered in agricultural lands did not excavate food as did geese wintering in coastal marshes.

In this paper, I (1) examine habitat-related variation in external morphology of Lesser Snow Geese from the midcontinent of North America, (2) discuss possible causes of this phenotypic variation, (3) consider this variation in relation to increased population size, and (4) discuss the relationship of this variation to other aspects of both the wintering and breeding ecology for this population of Lesser Snow Geese.

METHODS

Collection and measurement of geese.—Lesser Snow Geese in adult plumage were captured with rocket nets or shot, under permit for scientific collection, each winter (January to March) of 1983 and 1984 at eight locations in three landscapes (Fig. 1): (1) Marsh: Rockefeller State Wildlife Refuge (SWR) in Louisiana (January and February 1983, February 1984), Sabine National Wildlife Refuge (NWR) in Louisiana (January and February 1983 and 1984), and J. D. Murphree Wildlife Management Area (WMA) in Texas (January and February 1983 and 1984). (2) Rice Prairie: from within 16 km of the town of Garwood in Texas or Lacassine NWR in Louisiana (January and February 1983). (3) Corn: along the

Missouri River near Riverton, Iowa (January 1983, February 1984), near Schell City, Missouri (January 1984), or near Boyle, Kansas (February 1983).

On the day of collection, I measured culmen to the nearest 0.1 mm with calipers, and each bird was placed in a plastic bag and frozen. Birds were thawed to take nine additional linear measurements (wing length, tarsus bone length, body length, keel length, skull length, skull width, skull height, bill height, bill width) to the nearest 0.1 mm and to count number of serrations along one side of the upper mandible. Geese in adult plumage with a bursa of Fabricius were called subadult and those without were called adult (Hochbaum 1942). Details on study areas and morphological measurements were provided by Alisauskas (1988).

Band recoveries.—I compared recovery location with banding location for geese captured or shot that were wearing a United States Fish and Wildlife Service leg band. Recoveries were chosen for analysis if (1) banded in Nebraska, Iowa, Kansas, Missouri, Texas or Louisiana, (2) banded and recovered in December, January or February, (3) recovered in marsh, rice or corn landscapes (Fig. 1), and (4) were indirect recoveries (i.e. not recovered the winter of banding). Banding and recovery coordinates were defined as centers of 10-minute blocks of latitude and longitude, and superimposed on mapped landscapes (Fig. 1) with a Geographical Information System, thereby assigning landscapes of banding and recovery to locations.

Winter population indices.—I used data from Dzubin et al. (1975), Boyd et al. (1982), and the U.S. Fish and Wildlife Service (Waterfowl Population Status 1995 unpubl. data) to summarize annual winter counts of midcontinent Snow Geese, 1950/51 to 1993/94. These data were gathered in either December or January in the following states: Colorado, Kansas, Nebraska, New Mexico, Oklahoma, South Dakota, Texas, Alabama, Arkansas, Illinois, Indiana, Iowa, Kentucky, Louisiana, Michigan, Minnesota, Mississippi, Missouri, Ohio, Tennessee, and Wisconsin.

Statistical analyses.—I used multivariate methods to analyze morphometric variation in Lesser Snow Geese by winter habitat. Multivariate analysis of variance (MANOVA) is superior to several univariate tests for evaluating overall group differences because it uses rather than ignores correlations among characters (Willig et al. 1986). For MANOVA, I began with a saturated model containing four main effects (age, sex, year, landscape) and all possible interactions (PROC GLM/MANOVA; SAS 1990). Nonsignificant interactions were removed from the model, and the analysis was redone. Finally, nonsignificant main effects were removed from the model, resulting in a most-parsimonious model containing only effects that were significantly related to overall morphology. *A posteriori* contrasts (Student-Newman-

Keuls [SNK]) were done on each metric variable by winter landscape for each sex separately (Appendix).

I tested heterogeneity of within-landscape covariance matrices with Bartlett's modification of the likelihood-ratio test (PROC DISCRIM POOL = TEST option; SAS 1990). Input data were residuals from MANOVA of morphological variables in relation to year of collection, sex, and year \times sex interaction effects. Thus, residuals retained variation in morphology related to landscape from which geese were collected. The determinant of these matrices provides a measure of multivariate dispersion (Alisauskas 1987). When heterogeneity is significant, power of the MANOVA may be compromised thereby increasing risk of Type II error, but if the null hypotheses tested with MANOVA is rejected, violation of the assumption of heterogeneity is of less concern (Hatcher and Stepanski 1994).

I did principal components analysis (PCA) using the correlation matrix of 10 original metric variables to construct one index of body size and 9 indices of shape (see Results). Rexstad et al (1988) urged caution when using PCA and raised the question: "what criteria should be used to assess the number of important factors, or the interpretation of those factors with biological data?" Part of their concern had to do with the blind use of PCA and the risk of inappropriately conferring biological meaning on random data. Often, the importance of components is evaluated according to the proportion of variance explained by using, e.g. the "eigenvalue-one" criterion or the "scree-test" (Hatcher and Stepanski 1994), whereby PCs that explain a small amount of variance in the original data are discarded. However, the percentage of variance explained in PCA and biological meaning are not synonymous. Pimentel (1979:68) points out that "rejecting the last few principal components as meaningless can omit important biological features." Ricklefs and Miles (1994) recommend examination and retention of all PCs because smaller PCs can contain ecologically relevant information. This is the approach used in this paper.

I used Anderson's (1963) test for sphericity on eigenvalues 9 and 10 to test the hypothesis that all PCs are of equal magnitude ($\chi^2 = 1,484.8$, $df = 2$, $P < 0.0001$) and concluded that PCs were not arbitrarily derived. Furthermore, I randomly resampled 350 records of the 639 available in my data set, did PCA on the subset of records, and repeated this with replacement until 700 iterations were completed. From these 700 iterations I calculated the mean of each element in each eigenvector and compared this estimate with the estimate derived from the complete data set. The correspondence was virtually complete, further supporting results of the sphericity test that suggested the PCs were not arbitrarily derived. Finally, as an ad-hoc check, I calculated shape indices for each bird as $I = \Sigma(e+)/\Sigma(e-)$, where $e+$ are elements >0 and $e-$ are elements <0 that were considered to be im-

portant (see Table 2). As expected, I found high correlations (range 0.76 to 0.93, $n = 700$, $P < 0.0001$ in all cases) between these indices of shape and respective PC scores and so concluded that my interpretations of shape were appropriate.

I proceeded to test hypotheses of geographic variation in size and shape with respect to landscape by using PC scores as 10 independent and uncorrelated morphological indices for input data in MANOVA (PROC GLM/MANOVA; SAS 1990); landscape was the source of variation of interest, but I included sex, year and all interactions in the model to control for their effects. Following this protocol, I arrived at the most-parsimonious model by iteratively deleting nonsignificant interactions and then nonsignificant main effects. The resulting model included sex, year, landscape, and sex \times landscape interactions as significant effects. I then examined corresponding univariate ANOVAs of each principal component and present results only from those (i.e. PC1, PC2, PC6, PC10) that showed significant variation in relation to landscape following significant SNK tests. If significant variation in PC scores existed with respect to year or sex in addition to significant landscape effects, SNK tests were done on each PC score by landscape either for each year or for each sex separately. I used likelihood-ratio chi-square tests (PROC FREQ; SAS 1990) to determine if landscape in which birds were banded was independent of that from which they were recovered.

RESULTS

Morphometric variation among locations within landscapes.—Geese of the same sex, age, and collected in the same years but from different localities in brackish marsh (Rockefeller SWR, Sabine NWR, and J. D. Murphree WMA) did not, on average, differ morphologically (MANOVA, $F = 1.519$, $df = 22$ and 562 , $P = 0.061$). Geese from different sites in rice prairies (Garwood vs. Lacassine) also did not differ morphologically (MANOVA, $F = 0.726$, $df = 22$ and 182 , $P = 0.713$) after variation due to age and sex were accounted for. Such nearly significant variation within landscapes may have rendered tests among landscapes to be conservative. I did not test for morphological variation in geese from different sites in northern landscapes dominated by corn because collections were made from different sites in different years. Henceforth, data from different sites were pooled according to marsh, rice prairie or corn landscapes.

Multivariate analyses of variance in morphology.—Subadults were not distinguishable from

adults using MANOVA, so age classes were pooled. No significant interactions existed among sex, year, or landscape effects on the overall morphology of geese, indicating that the effects were independent and additive. Thus, MANOVA was redone with only sex, year, and landscape as terms in the model (Table 1); after controlling for significant variation in related to sex and year of collection, there were significant landscape effects on overall morphology of geese.

Univariate analyses of variance in morphometrics.—When each morphological variable was considered alone with three-way ANOVA, all measurements except serration number were different between sexes (Table 1, Appendix). Only tarsus length, skull width, bill height, and bill width varied between years. All variables except wing and body lengths varied among landscapes, after accounting for all other effects in each model (Table 1, Appendix).

Heterogeneity in morphological variance among landscapes.—Covariance matrices of residuals corrected for annual or sexual variation were heterogeneous ($\chi^2 = 429.1$, $df = 133$, $P < 0.0001$). Natural logarithms of determinants, which provide a measure of dispersion in covariance matrices, were 20.6 for geese from marsh, 24.3 from rice, and 21.8 from corn. Taken with results on differences in size and shape, these results indicate that geese from coastal marshes were largest and least variable in morphology, geese from rice prairie areas were intermediate in size but highly variable, and geese from northern landscapes dominated by corn were smallest in size and of moderately variability.

Analysis of size and shape using principal components.—Four PC axes (Table 2) varied in relation to landscape independently of one another, although MANOVA also demonstrated significant variation among landscapes in all PC scores when evaluated simultaneously (Table 3). Student-Newman-Keuls tests indicated that geese from marshes were largest in body size (PC1). Also, marsh geese had the thickest bills (PC2), the longest skulls and culmens (PC6), and the longest culmens relative to skull length (PC10, Fig. 3).

Recoveries of banded birds.—Landscapes that geese were recovered from were related to landscapes in which geese were banded (likelihood ratio, $\chi^2 = 472.1$, $df = 4$, $P < 0.001$; Table

TABLE 1. P-values from multivariate (MANOVA) and univariate (ANOVA) analyses of variance for 11 morphological variables of 639 Lesser Snow Geese with adult plumage by sex (male, $n = 310$; female $n = 329$), year (1983, $n = 383$; 1984, $n = 256$), and landscape (marsh, $n = 314$; rice prairie, $n = 200$; corn, $n = 125$).

Source	MANOVA	ANOVA										
		Wing length	Body length	Keel	Tarsus	Skull length	Skull width	Skull height	Culmen	Bill height	Bill width	Serrations
Sex	<0.0001	0.0009	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0018	ns
Year	<0.0001	ns	ns	<0.0001	ns	ns	0.0008	ns	<0.0001	<0.0001	<0.0001	ns
Landscape	<0.0001	ns	ns	0.0046	<0.0001	0.0362	0.0156	<0.0001	<0.0001	<0.0001	0.0012	ns

ns, $P \geq 0.05$.

TABLE 2. Principal components analysis of 10 morphological variables in midcontinent Lesser Snow Geese. Only PC whose scores varied significantly in relation to winter landscape (see Table 3) are shown. Elements in bold correspond to variables judged to covary the strongest with each PC.

Variable	Principal component			
	PC1	PC2	PC6	PC10
Wing length	0.22	-0.13	-0.03	0.01
Body length	0.29	-0.05	0.16	0.07
Keel	0.35	-0.11	0.25	0.11
Tarsus	0.34	-0.31	-0.17	0.02
Skull length	0.40	0.03	-0.36	-0.80
Skull width	0.33	-0.11	0.42	0.08
Skull height	0.33	-0.23	0.29	0.01
Culmen	0.37	0.01	-0.64	0.57
Bill height	0.28	0.49	0.29	0.04
Bill width	0.19	0.76	-0.04	0.04
% variance explained	49	11	5	2

4). Geese from rice were most philopatric (72%) to the landscape in which they were last captured compared to geese from marshes (56%) and those from corn landscapes (43%).

DISCUSSION

PROCESSES FOR MORPHOLOGICAL VARIATION BY WINTER LANDSCAPE

The mechanism by which geographic variation in morphology arose in midcontinent Lesser Snow Geese remains to be confirmed. Five not mutually exclusive hypotheses are presented to account for nonrandom distribution of morphs differing in size and shape among landscapes in their winter range: (1) differences in phenotypic selection among landscapes, (2) morphologically-based habitat selection, (3) landscape differences in nutrition of growing geese, (4) fall migration endurance of different-sized geese, and (5) differential rates of introgressive hybridization with Ross'

Geese (*Chen rossii*) among landscapes. Hypotheses 1 and 2 are based on the assumption that geographic variation in feeding morphology has an adaptive basis, and is related to winter food (see Owen 1980). Hypotheses 1 to 4 do not require necessarily that phenotypic variation has some underlying genetic basis, although it may be relevant to phenotypic and habitat selection, and to migration endurance. The possibility that part of the morphological variation among habitats is an outcome of introgressive hybridization with Ross' Geese assumes a genetic basis.

Phenotypic selection hypothesis.—Snow Geese collected from recently-invaded agricultural landscapes were different in mandibular morphology and body size than those from coastal marshes. Geese from marshes were rhizivorous (i.e. foraged by excavating roots, rhizomes or tubers; Alisauskas et al. 1988) and wintered in a habitat providing food resources best exploited with a thick, chisel-like bill (Bolen and Rylander 1978, Owen 1980). However, following winter range expansion that included new winter habitats with very different arrays of food that are palatable to Snow Geese, new opportunities emerged for winter sustenance. These include the ability of size morphs that may not have been well adapted for rhizivory (a prerequisite for survival in coastal marshes; Alisauskas et al. 1988), to settle onto winter habitats in which granivory and grazing of green vegetation, rather than rhizivory, are major foraging methods. In northern landscapes dominated by corn habitat, geese primarily foraged on agricultural seeds rather than on below-ground portions of plants, whereas geese in former rice prairies consumed the greatest diversity of foods (Alisauskas et al. 1988), which corresponds with them having the greatest diversity in morphology.

A predictable outcome of reduced selection is

TABLE 3. *P*-values from univariate analysis of variance by sex and winter landscape on principal components scores. PC analysis (see Table 2) was of 10 morphological variables measured on midcontinent Lesser Snow Geese.

Source	MANOVA	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Sex	<0.0001	<0.0001	ns	ns	0.0035	ns	0.0140	ns	0.0207	ns	ns
Year	<0.0001	ns	<0.0001	0.0009	ns	<0.0001	ns	0.0027	0.0051	0.0116	ns
Landscape	<0.0001	<0.0001	0.0031	ns	ns	ns	0.0037	ns	ns	ns	0.0009
Sex × landscape	0.0081	ns	ns	ns	ns	—	—	0.0016	0.0098	ns	ns

ns, *P* ≥ 0.05.

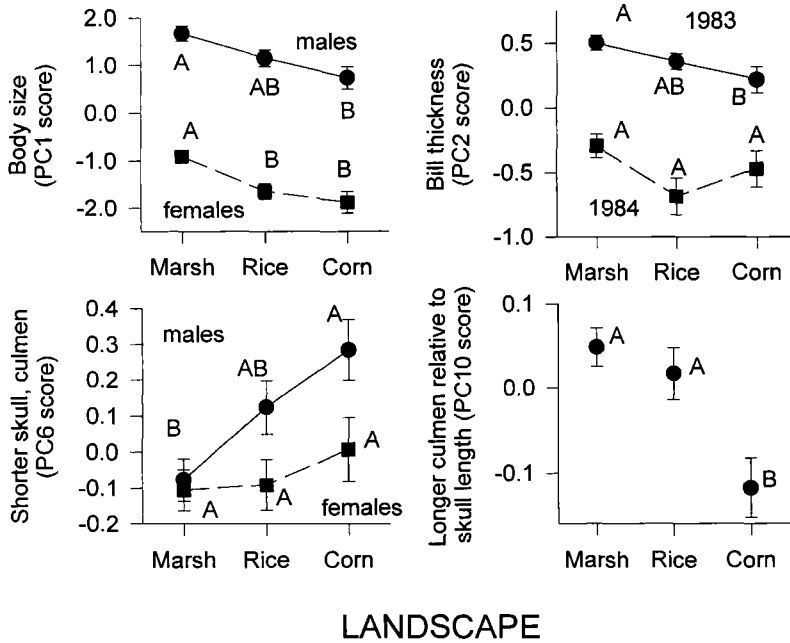


FIG. 3. PCA scores derived from 10 morphological variables measured on midcontinent Lesser Snow Geese summarized by winter landscape. Only PC scores (Table 2) significantly different among landscapes (three-way ANOVA in Table 3 followed by Student-Newman-Keuls tests) are shown.

that, from a continental perspective of composite mortality, survival should have increased. In fact, Francis et al. (1992) demonstrated that adult annual survival for a subset of the mid-continent population increased significantly from about 78% in 1970 to 88% by 1987. Enhanced survival may have been due to reduction in "natural" mortality resulting from winter range expansion and shifts in adaptive morphologies, as hypothesized above. However, landscape-specific patterns of mortality for geese of different morphologies are required to test this. Marking studies to examine size-based patterns of mortality and dispersal from each landscape may resolve whether phenotypic selection on body size or habitat selection

by different-sized birds (see below) are important determinants of observed geographic patterns in morphology.

If phenotypic variation among landscapes was genetically based, then life-history traits associated with reduced gene flow should have hastened geographical divergence in morphology. Differences in morphology documented herein arose in a relatively short period (12 to 20 years). Return of subadult geese to winter locations occupied as juveniles would tend to increase genetic differences among winter habitats and accelerate any genetically based divergence in phenotypes resulting from selection. Homing by adult Snow Geese to winter areas was evident in this study (Table 4). These data do not provide an estimate of the magnitude of gene flow, but suggest that the rate of gene flow is less than random. Examination of genetic structure in midcontinent Snow Geese from different landscapes may shed additional light on the underlying basis of the morphological differences.

Habitat-selection hypothesis.—Although homing to winter areas was evident between years (Table 4), short-term movements between hab-

TABLE 4. Recoveries of Lesser Snow Geese with respect to banding location at least one year before recovery.

Landscape banded	Landscape recovered		
	Marsh	Rice	Corn
Marsh	1,252	811	167
Rice	125	417	34
Corn	40	92	99

itats can occur in response to unfavorable weather. In 1984, for example, a southward exodus of geese from corn habitats occurred in apparent response to heavy snowfall and reduction in food availability (Alisauskas 1988). Severe frosts and inadequate rainfall may reduce availability of green grass to geese in rice habitats (Alisauskas et al. 1988); when this happens, some birds move from agricultural to marsh habitats (Alisauskas et al. 1988, 1998). During such movements, individual birds will have encountered different foods. Thus, some Snow Geese may sample a variety of habitats, and eventually settle in one that is most suited to their feeding morphologies. Such movements may have accounted for significant differences in morphology of geese sampled from the same landscape in different years (Table 1).

Nutrition hypothesis.—Diet quality varies considerably among landscapes considered in this study, and composite diets of geese wintering outside of coastal marsh habitats may contain inadequate minerals or an imbalance of specific amino acids (Alisauskas et al. 1988). If skeletons of juvenile Snow Geese continue to grow during their first winter, then diet deficiencies may affect asymptotic size. Hobaugh (1984) showed that juvenile Snow Geese in rice prairies were smaller than adults in culmen, wing, and tarsus length, suggesting that skeletal growth may not be complete until after the first winter (although the difference also could be due to phenotypic selection against large individuals in their first year). However, growth appears to be complete by May (Wypkema and Ankney 1979). Because environmental effects experienced during the first winter while growth is still occurring may have permanent effects, poor nutrition for a growing juvenile may explain why Snow Geese from corn habitats are structurally smaller than rice or marsh geese. To my knowledge, no reports exist of continued growth in wintering Snow Geese using repeated measures from recaptured birds.

Migration-endurance hypothesis.—Spring nutrient reserves are related to structural size in Lesser Snow Geese (Alisauskas 1988). If the same relation holds in fall, then smaller migrants may not have sufficient energy reserves to fly as far as larger Snow Geese. Thus, the inverse relation between body size and winter latitude also may be an outcome related to variable migration endurance in relation to size.

This could explain the relatively small size of geese from northern corn-dominated landscapes, but seems unlikely to account for differences between geese from contiguous marsh and rice landscapes.

Introgressive hybridization hypothesis.—Geographic variation in body size and bill size of Lesser Snow Geese could be due to gene flow from smaller Ross' Geese. Wintering Ross' Geese were comparatively rare in the midcontinent before the 1970s, when the bulk of the population wintered in the lower San Joaquin Valley, California (Bellrose 1976). Numbers of Ross' Geese in the midcontinent have increased (Prevett and MacInnes 1972, Frederick and Johnson 1983), and they are known to hybridize with Lesser Snow Geese (Trauger et al. 1971, Prevett and MacInnes 1972). After 1953, when the first Ross' Goose was seen in east Texas (Buller 1955), their numbers there had increased to between 103 and 541 birds by the late 1960s (Prevett and MacInnes 1972), 27,000 by 1991 to 1992 (Harpole et al. 1994) and >50,000 in 1994 to 1995 (Brian Sullivan, Texas Parks and Wildlife Department pers. comm.). In 1983 and 1984, Ross' Geese were frequently observed mixed in flocks of Lesser Snow Geese feeding in the rice prairies, but were never sighted on coastal marshes; on one occasion a Ross' Goose was observed courting a Lesser Snow Goose in rice habitat (Alisauskas unpubl. data). Harpole et al. (1994) reported that Ross' Geese comprised 9.9% of white geese surveyed in rice-prairie habitats compared to only 0.9% in coastal marshes. Numbers of Ross' Geese wintering farther north also have increased (Frederick and Johnson 1983), and breeding colonies of both Ross' Geese and Lesser Snow Geese nesting in the Central Canadian Arctic have increased greatly in number and size since 1976 (Alisauskas and Boyd 1994, Kerbes 1994). Recently greater overlap in ranges of Ross' Geese and midcontinent Lesser Snow Geese wintering in agricultural habitats has led to greater contact and possibly greater hybridization rates. Thereby, introgressive hybridization with Ross' Geese, that use both agricultural landscapes far in excess of brackish marsh habitats, may have contributed to smaller body size of Lesser Snow Geese that winter in agricultural landscapes. Examination of mitochondrial DNA of Lesser Snow Geese (see Avise et al. 1992) from different landscapes may ad-

dress the influence of introgressive hybridization with Ross' Geese.

CONSEQUENCES OF POPULATION GROWTH AND NONRANDOM SIZE DISTRIBUTIONS

Implications for fecundity.—Spring storage of nutrient reserves (Alisauskas 1988) is critical for breeding by Lesser Snow Geese (Ankney and MacInnes 1978). Potential clutch size of females was directly related to nutrient reserves during arrival at nesting areas (Ankney and MacInnes 1978); further, clutch size was correlated with culmen (an index of body size, Ankney and MacInnes 1978). In addition, evidence from other studies (Sedinger et al. 1995, Bon 1996, Choudhury et al. 1996) suggests that relationships between fecundity and body size may be pervasive in arctic-nesting geese, despite the inability to detect such a relation in Lesser Snow Geese nesting at La Pérouse Bay (Cooke et al. 1990, Cooch et al. 1992). The presumed mechanism for this relation is that body size constrains spring storage of nutrient reserves, thereby indirectly affecting fecundity (Alisauskas and Ankney 1990). Kirby and Obrecht (1982) suggested that Atlantic Brant (*Branta bernicla hrota*) from various winter areas may have different survival probabilities and fecundity. If fecundity is related to body size in Lesser Snow Geese, then demography of subpopulations of the midcontinent population may be specific to winter landscape.

Midcontinent decline in body size.—The rapid growth of the midcontinent population of Snow Geese since 1970 (Fig. 1) has had population consequences beyond winter areas. For example, crowding of Snow Geese on nesting areas has caused large-scale alteration of wetlands in the arctic (Kerbes et al. 1990). Vegetation destruction has had density-dependent effects on nutrition of geese resulting in a long-term decline in gosling growth rates, which, in turn, has led to smaller adults more recently near one breeding colony (Cooch et al. 1991); there was strong evidence that the shift toward smaller body size there was due to environmental rather than genetic causes. However, the adaptive phenotype hypotheses support the idea that small geese, regardless of the cause of variation in size, should more easily be accommodated in agricultural habitats than in traditional marsh habitats in winter. Formerly, di-

minutive geese would have been limited to coastal marshes during winter (McIlhenny 1932), and possibly experienced greater mortality compared to phenotypes adapted to marsh existence. Currently, small geese with proportionately smaller bills now can optionally settle on rice or corn habitats, thereby relaxing the inferred bottleneck in adaptive morphologies associated with strictly marsh existence. Adaptive phenotype hypotheses (1 and 2, above) are consistent with the correspondence between winter range expansion (Fig. 1) and population increase (Fig. 2), and with increased survival following range expansion (Francis et al. 1992). Thus, the shift toward smaller body size of midcontinent Lesser Snow Geese may have been assisted by expansion in winter range onto agricultural landscapes, in conjunction with density-dependent growth rates on breeding areas.

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APPENDIX. Morphological measurements ($\bar{x} \pm SD$, n in parentheses) of Lesser Snow Geese summarized by sex, year, and winter landscape. Student-Newman-Keuls *a posteriori* contrasts done by landscape separately for each sex in each year; means with different letters in superscript are significantly different ($p < 0.05$). All measurements are in mm.

Sex	1983			1984		
	Marsh	Rice	Corn	Marsh	Rice	Corn
			Wing length			
Male	437 ± 13.3 (86)	436 ± 11.9 (62)	432 ± 11.4 (39)	434 ± 12.7 (65)	428 ± 12.3 (31)	431 ± 16.3 (28)
Female	421 ± 10.0 (107)	419 ± 11.0 (75)	418 ± 11.5 (25)	414 ± 9.9 (66)	411 ± 15.1 (32)	414 ± 10.7 (31)
			Body length			
Male	183 ± 10.1 (86)	184 ± 11.4 (62)	182 ± 11.6 (39)	182 ± 7.8 (65)	184 ± 7.3 (31)	185 ± 9.5 (28)
Female	178 ± 9.7 (107)	177 ± 10.5 (75)	177 ± 7.9 (25)	177 ± 7.7 (66)	173 ± 10.0 (32)	175 ± 8.4 (31)
			Keel length			
Male	118 ± 5.0 (86)	117 ± 5.5 (62)	118 ± 5.8 (39)	118 ± 4.7 (65)	119 ± 5.2 (31)	118 ± 6.6 (28)
Female	113 ± 4.7 (107)	112 ± 4.5 (75)	113 ± 5.2 (25)	112 ± 4.9 ^A (66)	112 ± 3.6 ^A (32)	109 ± 4.6 ^B (31)
			Tarsus length			
Male	82.1 ± 3.9 ^A (86)	80.5 ± 4.3 ^B (62)	80.1 ± 4.0 ^B (39)	83.3 ± 3.3 (65)	83.8 ± 3.3 (31)	82.1 ± 3.9 (28)
Female	77.6 ± 3.8 (107)	76.9 ± 3.8 (75)	76.0 ± 3.4 (25)	79.7 ± 3.2 (66)	78.9 ± 3.2 (32)	78.8 ± 3.6 (31)
			Skull length			
Male	115 ± 5.3 (86)	115 ± 3.5 (62)	115 ± 4.3 (39)	116 ± 4.1 ^A (65)	114 ± 2.6 (31)	113 ± 3.9 ^B (28)
Female	111 ± 3.7 (107)	109 ± 4.1 (75)	111 ± 4.3 (25)	111 ± 3.6 ^A (66)	110 ± 4.1 (32)	109 ± 3.3 ^B (31)
			Skull width			
Male	37.8 ± 1.8 (86)	37.7 ± 1.2 (62)	38.0 ± 1.3 (39)	38.7 ± 1.3 (65)	38.4 ± 1.5 (31)	38.3 ± 1.5 (28)
Female	36.7 ± 1.5 (107)	36.3 ± 1.8 (75)	36.6 ± 1.4 (25)	37.0 ± 1.2 (66)	36.7 ± 1.3 (32)	36.4 ± 1.1 (31)
			Skull height			
Male	47.5 ± 1.8 ^A (86)	47.5 ± 1.6 ^A (62)	46.8 ± 1.7 ^B (39)	47.5 ± 1.7 (65)	47.9 ± 1.4 (31)	47.5 ± 1.8 (28)
Female	45.7 ± 1.3 (107)	45.1 ± 1.3 (75)	45.8 ± 1.4 (25)	45.8 ± 1.5 (66)	45.2 ± 1.6 (32)	45.4 ± 1.7 (31)
			Culmen length			
Male	58.5 ± 3.5 ^A (86)	57.8 ± 2.5 (62)	57.1 ± 2.6 ^B (39)	58.6 ± 2.6 ^A (65)	57.3 ± 2.7 ^B (31)	55.9 ± 3.1 ^C (28)
Female	55.6 ± 2.4 (107)	54.9 ± 3.0 (75)	54.7 ± 3.1 (25)	56.1 ± 2.5 ^A (66)	54.6 ± 2.8 ^B (32)	53.6 ± 2.4 ^B (31)
			Bill height			
Male	30.8 ± 1.8 ^A (86)	30.5 ± 1.6 (62)	30.2 ± 1.8 ^B (39)	29.8 ± 1.4 ^A (65)	29.1 ± 1.6 ^B (31)	29.0 ± 1.4 ^B (28)
Female	29.8 ± 1.5 ^A (107)	29.0 ± 1.7 ^B (75)	28.7 ± 2.3 ^B (25)	28.2 ± 1.2 ^A (66)	27.7 ± 1.5 (32)	27.5 ± 1.2 ^B (31)
			Bill width			
Male	24.5 ± 1.9 (86)	24.6 ± 1.1 (62)	23.9 ± 1.3 (39)	24.0 ± 1.9 (65)	22.9 ± 1.7 (31)	23.7 ± 2.1 (28)
Female	23.8 ± 1.1 (107)	23.1 ± 1.2 (75)	23.4 ± 2.1 (25)	22.9 ± 1.6 (66)	22.7 ± 2.1 (32)	22.5 ± 1.8 (31)