GEOGRAPHIC VARIATION IN MIGRATORY BEHAVIOR OF GREATER WHITE-FRONTED GEESE (*ANSER ALBIFRONS*)

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ABSTRACT.—We studied the migration and winter distribution of adult Greater White-fronted Geese (*Anser albifrons frontalis*) radio-marked on the Yukon-Kuskokwim Delta (YKD) and Bristol Bay Lowlands (BBL) of Alaska from 1987 to 1992. The major autumn staging site for geese from both breeding areas was the Klamath Basin on the California/Oregon border. However, temporal use of this area differed markedly between populations. Geese from the BBL arrived at the Klamath Basin nearly 30 days before geese from the YKD and departed before most YKD geese had arrived. Ninety percent of BBL geese used the Klamath Basin in autumn, whereas 30% of YKD geese bypassed the Klamath Basin during autumn and instead flew directly to the Central Valley of California. Nearly all BBL geese migrated directly from the Klamath Basin to wintering areas in Mexico, bypassing the Central Valley. Ninety percent of the BBL geese wintered in Mexico, as opposed to <20% of the YKD geese. Wetlands of the Interior Highlands in the state of Chihuahua, particularly Laguna Babicora, were used by >90% of the radio-marked geese in Mexico. Marshes along the West Coast comprised the other important wintering habitat in Mexico. The Sacramento Valley of California was the predominant wintering area for YKD geese. BBL geese migrated north from Mexico into the San Joaquin Valley or Sacramento-San Joaquin Delta of California by the last week of January. Fifty-five percent of the BBL population used the Klamath Basin in spring, but many birds staged in eastern Oregon and western Idaho. In contrast, geese from the YKD staged almost exclusively in the Klamath Basin during spring before flying to staging areas in Alaska. Breeding allopatry and temporal partitioning on staging and wintering areas likely has contributed to the evolution of previously described phenotypic differences between these populations. These two populations, along with the Tule Greater White-fronted Goose (*A. a. gambeli*), may constitute a portion of a Rassenkreis, a group of subspecies connected by clines, each ecotype of which has independent conservation needs. *Received 1 March 1996, accepted 12 June 1996.*

GEOGRAPHIC VARIATION in morphological and ecological characteristics is found in nearly every group of organisms and generally is considered an important element of species evolution (Endler 1977, Barrowclough 1982, Zink and Remsen 1986, Zink 1989). Despite numerous studies describing geographic variation in North American birds, little information exists for many species, especially migratory waterfowl. This is partly because geographic variation generally is less common in migratory compared with more sedentary species (due to potentially higher rates of gene flow among populations of highly mobile animals), but also because the breeding areas of many wintering waterfowl populations are not known.

The Greater White-fronted Goose (*Anser albifrons*) is one of the most widely distributed waterfowl species in the arctic (Ploeger 1968, Ely and Dzubin 1994). Early observations and morphological studies (see Krogman 1979, Zink and Remsen 1986) led to the designation of two subspecies of white-fronted geese in North America (AOU 1957, Sibley and Monroe 1990). The Tule White-fronted Goose (*A. a. gambeli*) nests only in the vicinity of Cook Inlet, Alaska, and winters in the Central Valley of California (Timm et al. 1982). The other North American subspecies, *A. a. frontalis*, is composed of Pacific and mid-continent populations, and nests from the Bering Sea across the arctic to Hudson Bay, Canada (Timm and Dau 1979, Bellrose 1980, Pacific Flyway Study Committee 1987). The Pacific and mid-continent populations of *frontalis* are nearly completely segregated. Geese that nest

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on the Yukon-Kuskokwim Delta (YKD) in Alaska migrate to the Pacific states and Mexico, but geese nesting at more northern and eastern locations in Alaska and Canada migrate through the Central Flyway and winter primarily in Texas, Louisiana, and central and eastern Mexico (Miller et al. 1968, Ely and Dzubin 1994, C. Lensink unpubl. data).

Here, we present results of a multiyear study of the migratory behavior and distribution of Greater White-fronted Geese from the YKD and the Bristol Bay Lowlands (BBL) of western Alaska, the two most important breeding areas for these geese in the Pacific Flyway (Bellrose 1980). Our work was stimulated by population declines of Greater White-fronted Geese in the Pacific Flyway (Raveling 1984) and earlier work that revealed potential differences in migration ecology between subpopulations (Ely and Raveling 1989, C. Lensink unpubl. data). We present information on radio-marked geese followed throughout the year during spring and autumn migrations among Alaska, California, and Mexico. We also document temporally segregated but geographically sympatric distributions on a key autumn migration area and provide evidence that Greater White-fronted Geese are clinally distributed (Endler 1977).

METHODS

Capture and marking.—We herded molting geese into corral traps (Cooch 1953) with aircraft during June and July, 1987–1991, near Hook Lagoon on the Alaska Peninsula (south BBL; 57°10′N, 158°10′W), on the Nushagak Peninsula (north BBL; 58°20′N, 158°50′W), and near the Kashunuk and Manokinak rivers on the central YKD (61°20′N, 165°20′W; Fig. 1). We determined the age and sex of all geese captured, and weighed and measured most adults (Orthmeyer et al. 1995). Females were selected for radio marking for a concurrent study of survival. Geese were marked with U. S. Fish and Wildlife Service (USFWS) leg bands, and either a 45-g transmitter attached to a backpack harness (1987 and 1988) or a 30-g solar transmitter glued to a yellow plastic neck collar individually identified with black digits (Ely et al. 1993). Transmitter life was about 14 months for backpack radios and 24 months for solar radios.

Telemetry tracking.—We located radio-marked geese from trucks equipped with 4-element Yagi antenna systems and also from fixed-wing aircraft. Radio tracking was conducted during summer in Alaska, and from late August through April in California, Oregon, and Mexico. Radio tracking was most intensive during autumn in the Klamath Basin of Califor-

nia and Oregon and in the Northern Interior Highlands in the State of Chihuahua, Mexico. During winter, we concentrated our radio-tracking efforts in the Klamath Basin, the Northern Interior Highlands, and in the Central Valley of California. Details of monitoring radio-marked geese are provided in the Appendix.

Neck-banded geese.—Use of areas north of the Klamath Basin during spring was determined from observations of neck-banded geese (Ely 1990). We marked geese with coded neck-bands during 1979 through 1981 and again during 1986 through 1992 in the Klamath Basin of California and on the two breeding areas in Alaska. Geese captured in the Klamath Basin before 1 October were assumed to be of BBL origin, whereas those caught later were considered part of the YKD population (see Results). Cooperators read neck-band codes in the Columbia River Basin of Oregon and Washington, central and eastern Oregon, western Idaho, and parts of Alaska. The distribution of neck-banded geese from BBL versus YKD was compared with chi-squared analyses (SAS Institute 1989). In addition, we obtained information on the recovery of all Greater White-fronted Geese banded on the YKD and reported to the Bird Banding Laboratory before September 1994. We used chi-squared analyses to determine differences in recovery distributions of geese leg-banded at different locations on the YKD.

Length-of-stay estimates.—The length of time geese stayed in the Klamath Basin during autumn was estimated from the dates of arrival and departure of radio-marked geese. Only radio-marked geese subsequently located outside of the Klamath Basin were used in the analyses to prevent inflating length-of-stay estimates by including data from geese that lost transmitters or died during the study but were not relocated. Differences between populations were examined with analysis of variance (ANOVA) and paired-*t* tests (SAS Institute 1989).

Population size and productivity.—We estimated the sizes of the BBL and YKD populations based on autumn surveys in the Klamath Basin (Klamath Basin National Wildlife Refuges, USFWS unpubl. data) and two separate breeding pair surveys (1957–1994 and 1993–1994) on the YKD and BBL in Alaska during summer (Migratory Bird Management Office, USFWS unpubl data). Productivity was estimated from age-ratio counts of flocks in the Klamath Basin during September and October 1979–1981, before the hunting season began (Ely 1993).

RESULTS

Capture, banding, and re-observations.—A total of 244 adult geese was radio-marked at three sites in western Alaska (Table 1); 18 additional geese included in our analyses were radio-marked during September and October in the
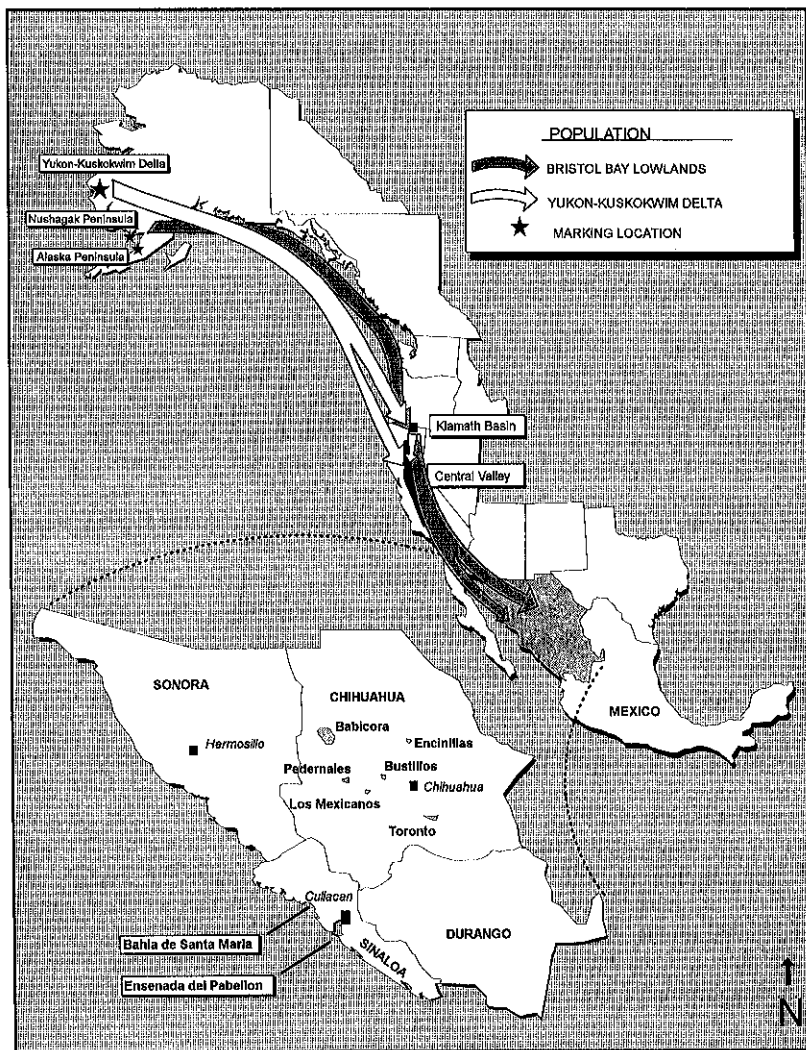
FIG. 1. Autumn migration and wintering areas of radio-marked Greater White-fronted Geese from two breeding areas in western Alaska.

Klamath Basin and were later located on breeding areas in Alaska. Geese captured at BBL sites likely were nonbreeders or unsuccessful nesters, because we observed no immature (i.e. local) geese at the banding sites. Fifty-one (84%) of the 61 geese radio-marked on the YKD were captured at nests or were in brood flocks; the remainder were in flocks without young and were assumed to be either nonbreeders or unsuccessful nesters. We relocated 204 (84%) of the 244 radio-marked geese south of Alaska, including 82% of YKD geese and 84% of BBL geese. Thirty-two radio-marked geese were monitored for two or more years.

Autumn migration.—The Klamath Basin was the primary autumn staging area for geese after migration from Alaska (Fig. 1). Four radio-marked BBL geese were located along the coasts of Washington and Oregon in August and September of 1988, but in general, areas north of the Klamath Basin were rarely used in autumn. Geese from the two BBL sites did not differ in dates of arrival at ($F = 0.01$, df = 1 and 149, $P = 0.92$) or departure from ($F = 1.28$, df = 1 and 132, $P = 0.26$) the Klamath Basin, so we pooled these data for analyses (Table 2). Geese with backpack radios arrived in the Klamath Basin later ($F = 7.64$, df = 1 and 169, $P = 0.006$) and

TABLE 1. Number of Greater White-fronted Geese (by sex) radio-marked in western Alaska during the summers of 1987 through 1991. Breeding areas include the Alaska (South) and Nushagak (North) peninsulas of the Bristol Bay Lowlands (BBL) and the central Yukon-Kuskokwim Delta (YKD).

Year of marking	BBL						YKD	
	South		North		Total			
	M	F	M	F	M	F	M	F
1987	0	0	0	0	0	0	1	11
1988	3	12	2	5	5	17	1	16
1989	0	15	0	15	0	30	9	15
1990	11	10	3	47	14	57	2	6
1991	0	0	0	60	0	60	0	0
Total	14	37	5	127	19	164	13	48

left later ($F = 36.06$, df = 1 and 145, $P < 0.001$) than geese wearing neck-collar radios, so data from backpack radios are not included in statistical comparisons in use of the Klamath Basin. Geese from the BBL arrived in the Klamath Basin in early September each year, nearly a month in advance of geese from the YKD (Table 2). This difference was highly significant ($F = 107.17$, df = 1 and 148, $P < 0.001$). No differences were noted among years ($F = 1.54$, df = 2 and 148, $P = 0.219$).

The timing of arrival of individual geese at the Klamath Basin was not consistent between years. For example, only 8 of the 16 radio-marked geese for which we had arrival times for two years were consistent in arriving either before or after the mean arrival date of other radio-marked geese from the same breeding area. There also were no differences in arrival times between breeding ($\bar{x} = 7$ October ± SE of 1.29 days) and nonbreeding birds ($\bar{x} = 9$ October ± 0.50 days), although samples were small ($F = 0.77$, df = 1 and 6, $P = 0.422$).

Ninety percent (140 of 156 different radio-marked geese located south of Alaska) of BBL geese used the Klamath Basin during September, with 85–93% of BBL geese then bypassing the Central Valley of California and flying to either the Northern Interior Highlands or west coast of Mexico by late September (Figs. 1, 2). In contrast, only 70% (35 of 50) of YKD geese stopped in the Klamath Basin; the other 30% flew directly to the Central Valley. YKD geese that stopped in the Klamath Basin usually remained until December and then moved south to the Central Valley.

Winter distribution.—Geese of BBL origin were much more likely than YKD geese to winter in Mexico (Fig. 2). Initial relocations of radio-marked geese in Mexico were reported by co-operators who relocated two geese at Laguna de Babicora, Chihuahua in 1988 (R. Drewien and J. Taylor pers. comm.) and one bird on the west coast in January in 1988 and 1989 (B. Conant pers. comm.). We searched these regions of Mexico in December 1989 and relocated 18 of 24 radio-marked geese from the BBL population, 16 of which were in the Northern Interior Highlands, one on the west coast, and one at both locations (Fig. 1). Surveys in Mexico were more complete in 1990 to 1991 and 1991

TABLE 2. Timing of arrival to and departure from the Klamath Basin of California during autumn by radio-marked Greater White-fronted Geese from two breeding areas in western Alaska.

Year	Date of arrival			Date of departure			Length of stay (days)		
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
	Yukon-Kuskokwim Delta								
1987[a]	4	14 Oct	6.2	3	5 Nov	3.8	3	24.0	10.1
1988[a]	7	15 Oct	8.8	2	22 Dec	2.5	2	51.5	28.5
1989	7	8 Oct	1.0	6	27 Oct	11.1	6	19.0	10.4
1990	4	6 Oct	11.3	4	15 Oct	15.9	4	10.0	9.0
1991	1	13 Oct		0	—	—	0	—	—
Mean[b]		9 Oct			21 Oct			14.5	
	Bristol Bay Lowlands								
1988[a]	8	12 Sep	1.2	4	9 Oct	12.3	4	30.8	11.1
1989	19	8 Sep	1.7	18	17 Sep	1.8	18	11.7	1.8
1990	57	1 Sep	1.1	53	12 Sep	1.7	53	11.3	1.0
1991	66	5 Sep	1.0	59	13 Sep	1.1	59	9.1	0.7
Mean[b]		5 Sep			14 Sep			10.7	

[a] Radios attached with backpack harnesses; all other years radios glued to neck bands.

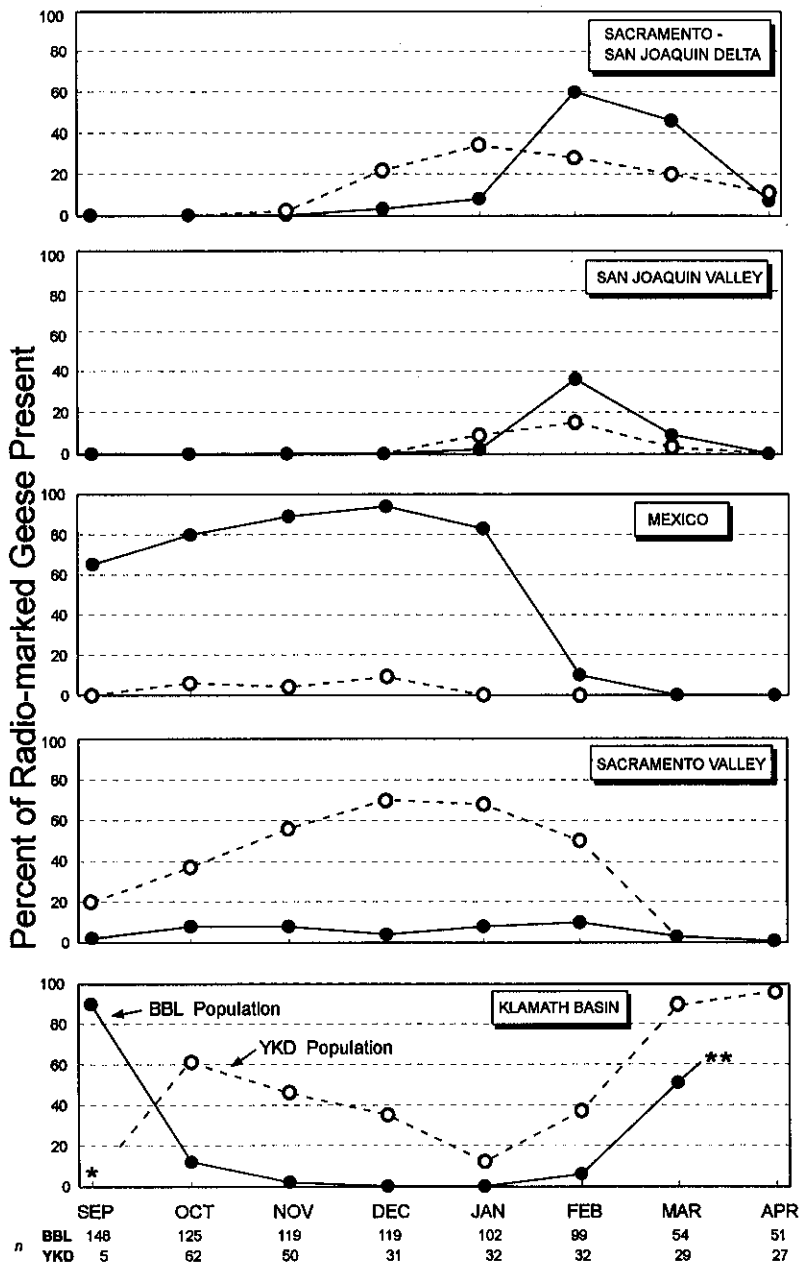[b] Mean does not include data from 1987 and 1988 when geese were wearing backpack radios.

FIG. 2.   Chronology of migration and distribution of radio-marked Greater White-fronted Geese from two breeding areas in western Alaska. Geese from the Bristol Bay Lowlands (BBL) and the Yukon-Kuskokwim Delta (YKD) are represented by solid and hatched lines, respectively. Most YKD geese did not arrive to the Klamath Basin until October, and many BBL geese staged north of the Klamath Basin in spring at areas where radios were not monitored (note asterisks in bottom panel; see Table 3).

to 1992. During these years, 93.8% of BBL geese were relocated in Mexico from October to January versus 18% of YKD geese ($\chi^2 = 77.9, 89.1, 81.9,$ and 66.9 for monthly proportions of BBL and YKD geese in Mexico during October to

January, respectively; all $Ps < 0.001$). Most (90%) BBL geese wintering in Mexico were found on wetlands of the Northern Interior Highlands. Of these, Laguna de Babicora was the most important, with more than 95% of radio-marked

TABLE 3. Differential use of northern migration areas in the Pacific Flyway by neck-banded Greater White-fronted Geese from two breeding areas in western Alaska during March through May, 1980–1993.

Location	Number of neck bands observed per population					
	Bristol Bay Lowlands[a]			Yukon-Kuskokwim Delta[b]		
	≤1986 (n = 150)	≥1987 (n = 629)	Total (n = 779)	≤1986 (n = 1,340)	≥1987 (n = 679)	Total (n = 2,019)
W. Oregon/Columbia R.	0	5	5	0	0	0
E. Oregon/Idaho	14	40	54	4	2	6
Pacific Coast[c]	0	0	0	29	1	30
Kodiak I./Alaska Pen.	6	8	14	1	1	2

[a] Includes geese marked at Nushagak and Alaska peninsulas and at Klamath Basin in September.
[b] Includes geese caught on the YKD and all geese captured in California and Oregon after 30 September.
[c] Includes coasts of Washington; British Columbia; Stikine Delta, Kenai Peninsula; and Cook Inlet, Alaska.

geese in the Northern Interior Highlands detected there during the winter. Laguna de los Mexicanos, Laguna de los Bustillos, Laguna Pedernales, Laguna de Encinillas, and Laguna Toronto (Fig. 1) all were used by radio-marked geese but never accounted for more than 10% of the Highlands population (Fig. 1). Radio-marked geese also were located along the west coast, particularly at Bahia de Santa Maria and Ensenada del Pabellon. Most BBL geese remained in Mexico until late January when they migrated north through the San Joaquin Valley to the Sacramento-San Joaquin Delta of California.

Interchange occurred between the two wintering areas in Mexico. Four radio-marked birds were relocated on both the west coast and Northern Interior Highlands during the same winter, including 1990–91, when three of seven radio-marked geese located on the west coast were also found in the Interior Highlands. Infrequent monitoring on the west coast of Mexico likely limited our ability to document movements of radio-marked geese between wintering areas.

The Sacramento Valley of California was the most important wintering area for YKD geese (Fig. 2). YKD geese began moving from the Sacramento Valley to the Sacramento-San Joaquin Delta as early as December, whereas BBL geese did not begin using the Delta until late January or early February (Fig. 2). Most (>80%) YKD geese migrated north to the Klamath Basin during February, but in some years, up to 20% remained on the Sacramento-San Joaquin Delta until March, where they foraged in mixed flocks with BBL geese returning from Mexico.

Spring migration.—The Klamath Basin was the predominant spring staging area for YKD geese and also was an important spring staging area

for BBL geese, although many of the latter apparently bypassed the Klamath Basin in March and April. We did not regularly monitor birds with radio-transmitters north of the Klamath Basin and were able to account for only approximately 50% of the BBL birds during March and April (Fig. 2). However, observations of neck-banded geese indicated that BBL geese used spring staging areas in central and eastern Oregon and western Idaho (Fig. 3, Table 3). BBL geese were much more likely to use staging areas in Oregon and Idaho than were YKD geese ($x^2 = 131.17$, df = 1, $P < 0.001$).

The two populations also used different stopover areas at the northern end of their migration route. YKD geese apparently flew along the northeast coast of the Gulf of Alaska, as they were observed at the Stikine River Delta, Kenai Peninsula, and Cook Inlet, Alaska, whereas BBL geese likely flew across the Gulf of Alaska, as indicated by observations on Kodiak Island and the lack of sightings elsewhere (Table 3, Fig. 3). BBL geese arrived at breeding areas on the Alaska Peninsula in early to mid-April (R. Wilk and D. Dewhurst unpubl. data) in contrast to YKD geese, which did not arrive in large numbers on the YKD until mid-May (Ely and Raveling 1984, C. Ely unpubl. data).

Relocation of radio-marked geese in Alaska.—Relocations of radio-marked birds the summer after banding confirmed the breeding affinity of BBL geese marked in molting flocks. During telemetry surveys in May of 1990 and 1991, we located 14 radio-marked geese on the south side of Bristol Bay that had been captured the previous summer in molting flocks on the Alaska Peninsula. Radio-marked geese were dispersed as singles or pairs and were located in wetland tundra habitats, suggesting that they were nesting.
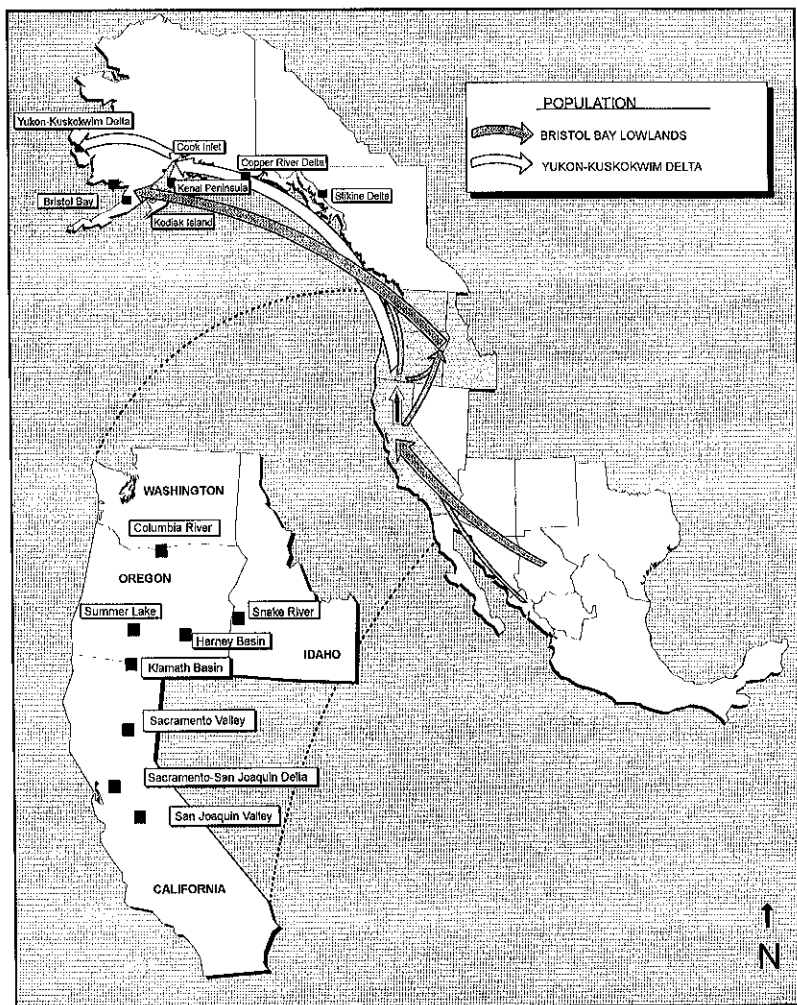
FIG. 3.   Spring migration of radio-marked and neck-banded Greater White-fronted Geese from two breeding areas in western Alaska.

There was limited movement of birds between the BBL and the YKD. Of 80 geese relocated in telemetry surveys of the BBL and YKD the summer after banding, 6 (7.5%) that originally had been marked in molting flocks in the BBL were found on the YKD, and 1 (1.2%) that originally was marked on the YKD was found on the BBL.

Population size and productivity.—Inventories during autumn in the Klamath Basin showed an increase in the number of Greater White-fronted Geese beginning in late August, with peak counts in late October to early November after the main arrival of geese from the YKD (Klamath Basin National Wildlife Refuges unpubl. data; Fig. 4). The departure of BBL geese in mid-September often was not apparent in the

counts because of overlap between early-arriving YKD geese and lingering BBL geese, although in 10 of 29 years weekly counts declined temporarily in the Klamath Basin during September. Maximum counts the first 10 days of September, when BBL geese were present, ranged from 22,000 in the 1950s and 1960s to 32,000 in 1990, compared with peak counts of YKD geese in late October to early November that varied from nearly 500,000 birds in the 1960s to 140,000 in 1993. Aerial breeding pair surveys conducted by the USFWS in Alaska during May and June indicated that BBL geese comprised from 4% (based on an extrapolated count of 30,900 birds; B. Platte and W. Butler unpubl. data) to 19% (based on a count of 22,700 birds; B. Conant and J. Hodges unpubl. data) of the
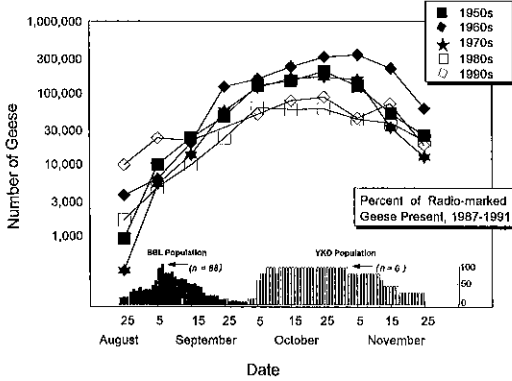
FIG. 4. Subpopulation composition of Greater White-fronted Geese during autumn in the Klamath Basin, showing maximum weekly counts (1955–1993), and percentage of radio-marked geese present (1987–1991) from two different breeding areas in western Alaska.

Greater White-fronted Geese in western Alaska (the known breeding areas for Pacific Flyway Greater White-fronted Geese; Bellrose 1980), with the remainder originating from the YKD.

The productivity of BBL and YKD geese has been similar, as determined by the proportion of young counted in flocks in the Klamath Basin. The proportion of young in flocks did not differ significantly ($F = 1.17$, df = 1 and 199, $P = 0.327$) between September, when BBL geese were present ($\bar{x} = 27.7 \pm 1.67\%$ young, $n = 105$ flocks) and October, when YKD geese were present ($\bar{x} = 30.3 \pm 1.39\%$ young, $n = 100$ flocks). Families were common among the earliest-arriving geese from both populations.

DISCUSSION

Temporal segregation. —Except for limited overlap in the timing of use of the Sacramento-San Joaquin Delta and the Klamath Basin in spring (Fig. 2), BBL and YKD geese were temporally segregated during much of their annual cycles. BBL geese were earlier spring migrants, and also apparently nested earlier than YKD geese, because sightings of Class I broods (Bellrose 1980) in the BBL the first week of June (R. Wilk unpubl. data), and Class II broods in early to mid-July (D. Dewhurst unpubl. data) indicated that hatching occurred in early June compared with late June to early July on the YKD (Ely and Raveling 1984). Similarly, Tundra Swans (*Cygnus columbianus*) also nest earlier at BBL than at YKD (Wilk 1988). Thus, early au-

tumn migration by BBL geese probably was an outcome of advanced breeding chronology.

Differences in breeding chronology likely ensure at least partial reproductive isolation, especially in arctic-nesting geese that rely heavily on body reserves acquired late in spring for reproduction (Ankney and MacInnes 1978, Ely and Raveling 1989). Differences in body composition among wintering YKD and BBL geese (Ely and Raveling 1989) may influence timing and allocation of reserves for reproduction and influence breeding chronology. Although the reproductive strategy of Greater White-fronted Geese may be more physiologically flexible than for many other species of arctic geese in being characterized by follicular development and substantial nutrient acquisition after arrival on the breeding grounds (Ely and Raveling 1984, Ely and Raveling 1989, Budeau et al. 1991), it seems unlikely that even such an elastic breeding strategy would enable individuals to adapt to such phenologically disparate breeding habitats as the YKD and BBL (see Raveling 1978). Temporal and geographic isolation probably has also minimized dispersal between populations. Allopatry may be especially important during spring and summer when pair formation may occur (Ely and Scribner 1994).

The discovery of temporal segregation among populations on the primary autumn staging area supports earlier evidence of interpopulation variation in migration chronology of Pacific Flyway Greater White-fronted Geese. In excess of 10,000 Greater White-fronted Geese pass through the Copper River Delta of southern Alaska (Fig. 3) in late August to early September (Isleib and Kessel 1973), and Hawkings (1982) speculated they represented the earliest of two or three different populations of geese that arrived in the Klamath Basin from late August to late October. Ely and Raveling (1989) reported that neck-banded geese migrating through the Klamath Basin in September and not reappearing in California until late winter likely wintered in Mexico, but at the time of their study they did not know the early migrants originated from the BBL.

Subpopulation discrimination. —Studies attempting to discriminate among subpopulations of waterfowl have met with variable success. Tacha et al. (1988, 1991) found no relationship between breeding and staging areas used by radio-marked Canada Geese (*Branta*

canadensis interior) wintering in the Mississippi Valley. Similarly, Maisonneuve and Bedard (1992, 1993) failed to find temporal or spatial structuring among subpopulations of staging and wintering Greater Snow Geese (*Chen caerulescens atlantica*). Other studies, however, have reported differences among populations of geese from different breeding areas in the use of staging and wintering areas including Canada Geese (Raveling 1979) and Brant (*Branta bernicla*; Reed et al. 1989a,b). Results of genetic studies also have been equivocal, with geographic structuring evident among Canada Goose populations (Shields and Wilson 1987, Van Wagner and Baker 1990), but less obvious in Lesser Snow Geese (*C. c. caerulescens*; Avise et al. 1992).

Our findings of subpopulation differences could be confounded by the fact that we were unable to capture breeding geese in the BBL region, as geese captured in that area may not have represented locally nesting birds (e.g. Lumsden 1975). We believe such a scenario is unlikely, however, because: (1) the relatively high proportion of immatures in the Klamath Basin in early September (see below) indicated that radio-marked geese arrived in flocks with breeding birds; (2) radio-marked breeding and nonbreeding geese from the same (YKD) population exhibited similar migration patterns; (3) breeding and nonbreeding geese leg-banded in the same area on the central YKD (the only location for which such data are available) showed similar recovery distributions (C. Lensink unpubl. data); and (4) radio-marked BBL geese returned to nearby nesting areas the summer following capture on the Alaska Peninsula. Female geese in general, show strong natal and breeding-site philopatry (Owen 1980).

Subspecies complex.—Greater White-fronted Geese exhibit considerable morphological variation and geographic structuring relative to many other species of waterfowl (Ely and Scribner 1994). In addition to the described variants from North America, subspecies breed in western Greenland (*A. a. flavirostris*) and across northern Siberia (*A. a. albifrons*), the latter of which is likely comprised of two or more separate populations (Ely et al. unpubl. data). Orthmeyer et al. (1995) found that Greater White-fronted Geese breeding in the BBL of southwestern Alaska were intermediate in size between Tule Geese and Greater White-fronted Geese from the YKD. Thus, there is ample evidence to suggest that the Greater White-front-

ed Goose complex constitutes a Rassenkreis—a group of subspecies connected by clines (Endler 1977)—of Holarctic distribution.

Discrete or clinal variation?—We marked birds at only two breeding locations and thus cannot determine whether ecological or morphological (see Orthmeyer et al. 1995) traits are discretely or clinally distributed (see Endler 1977, Barton and Hewitt 1989, James 1991). Additional evidence, however, suggests that traits of Greater White-fronted Geese in western Alaska are distributed clinally and that the Bristol Bay component does not represent a separate form, but is the southern end of a continuum. An analysis of the distribution of recoveries of Greater White-fronted Geese banded on the YKD reveals a latitudinal gradient in the proportion recovered in Mexico versus the Pacific states (C. Lensink unpubl. data). Geese banded at southern locations of the YKD are much more likely ($\chi^2 = 118.62$, df $= 2$, $P < 0.001$) to winter in Mexico (57 of 247 recoveries) than are geese from the central (13 of 614 recoveries) or northern YKD (0 of 76 recoveries).

The interchange of radio-marked individuals between the YKD and BBL, although limited, may be indicative of gene flow among populations, which would lead to clinal rather than discrete variation. Interpretation is difficult, however, because movements of individuals are not necessarily indicative of gene flow unless dispersing individuals breed successfully (Rockwell and Barrowclough 1987). Geese moving among breeding areas may simply have been undergoing molt migration, remaining segregated after arrival on the molting grounds.

Gene flow among populations has not been verified, although mixed subspecies families (*A. a. gambeli* and *A. a. frontalis*) have been observed (M. Wege and C. Ely unpubl. data). The relatively high intrapopulation variation in mensural characters reported by Orthmeyer et al. (1995) may be due to interbreeding, further suggesting clinal distribution.

Origin of populations.—Several scenarios may have led to the segregation of breeding populations of Greater White-fronted Geese in western Alaska. Snow and ice melt on the south side of Bristol Bay precedes that on the YKD by nearly a month, enabling early nesting and subsequent autumn migration. The BBL population simply could be comprised of wayward spring migrants originally destined for the YKD (but see above). The BBL was covered with ice dur-

ing the mid-Pleistocene, but the YKD was a refugium (Pewe 1975). Hence, the BBL was likely colonized by YKD geese, possibly to take advantage of earlier nesting opportunities. The presence of other unique migratory avifauna within the BBL supports the hypothesis that the area was isolated and/or recently (since the last glaciations) recolonized. Marbled Godwits (*Limosa fedoa*; Gibson and Kessel 1989) and Sandhill Cranes (*Grus canadensis*; Pogson 1987) probably are relict populations or recent immigrants to the region.

Separation of wintering populations.—Wintering areas in the Interior Highlands and west coast of Mexico are nearly 1,500 km south of the Central Valley of California, the major wintering area of Greater White-fronted Geese in the Pacific Flyway. This disjunction of wintering populations of Greater White-fronted Geese and other waterfowl in the Pacific Flyway (see Bellrose 1980) is at least partly due to loss of wetland habit. Destruction of marshes in southern California, and in particular, the loss of wetlands of the Colorado River Delta, has eliminated important staging and wintering habitats potentially linking the Central Valley of California and the wetlands of Mexico. California already has lost 95% of its wetlands (Katibah 1984), and many of the most important wetlands in Mexico are threatened (Sparrowe et al. 1989). The Laguna de Babicora marsh is one of the most important natural wetlands in central Mexico (Sparrowe et al. 1989, Leyva-Espinosa 1993). In addition to its importance to Greater White-fronted Geese, it provides habitat for considerable numbers of Lesser Snow Geese, Sandhill Cranes, Bald Eagles (*Haliaeetus leucocephalus*) Long-billed Curlews (*Numenius americanus*), and numerous species of Neotropical passerines (Saunders and Saunders 1981, R. Drewien unpubl. data). Migratory birds are highly adaptable, but further losses of already minimal wetland habitats could prove catastrophic, especially to small, highly site-faithful populations such as the Bristol Bay Greater White-fronted Goose.

Taxonomic status and conservation.—Considerable disagreement exists regarding the criteria necessary for designating subspecies (Mayr and Ashlock 1991, O'Brien and Mayr 1991). We have demonstrated distinct ecological and geographical separation among BBL and YKD geese, and Orthmeyer et al. (1995) found considerable morphological separation among these same populations. It is unclear, however, whether subspecies status is warranted given our contention that BBL and YKD geese are clinally distributed. We suspect that Greater White-fronted Geese are not unique in this regard, as few other studies have monitored intraspecific movements among breeding areas. Without taxonomic recognition, it may prove difficult to garner the support needed to adequately manage the BBL population. Our findings confirm the importance of identifying intraspecific variation in life history characteristics in ecological studies. Basic questions regarding behavior, physiology, survival, and conservation biology are unanswerable, or even worse, answered incorrectly, without an understanding of intraspecific variation in distribution and movements.

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APPENDIX. Timing and location of monitoring for radio-marked Greater White-fronted Geese in the Pacific Flyway, 1987 to 1992.[a]

Location	Season		
	Autumn	Winter	Spring
Klamath Basin			
Ground	Daily[b]	Daily[b]	Daily[b]
Air	Semi-monthly	Semi-monthly	Semi-monthly
Central Valley			
Ground	Daily[c,d]	Daily[d]	Daily[d,e]
Air	Monthly	Monthly	Monthly[e]
Mexico (Interior Highlands)			
Ground	Daily[f]	Daily[f]	—
Air	Semi-monthly[f]	Semi-monthly[f]	—
Mexico (west coast)			
Ground[g]	Intermittent	Intermittent	—
Air	Monthly	Monthly	—

[a] Does not include radio tracking in Alaska, which consisted of annual flights on the outer YK Delta and Bristol Bay Lowlands during May and June 1990–1992.

[b] Daily 1987–1990 and during autumn 1990–1992; weekly during winter/spring 1990–1992.

[c] Beginning approximately 1 November.

[d] Daily 1987–1990; semi-monthly 1990–1992.

[e] Ground surveys in the Central Valley ended ca. 15 March and air surveys ca. 15 April.

[f] Ground surveys late September through mid-January 1990–1992; air surveys mid-September through February 1990–1992. One ground and one air survey in December 1989. Areas other than Laguna de Babicora monitored semi-monthly. Autumn surveys not flown in 1991 until 4–5 October; this flight is included with the September survey data.

[g] Air and ground survey in December 1989. Monitored by cooperator from mid-August through mid-February, 1989–1992.