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MIGRATION AND HABITAT RELATIONSHIPS OF GEESE ON THE EASTERN
COPPER RIVER DELTA, ALASKA

UNIVERSITY OF ALASKA

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MIGRATION AND HABITAT RELATIONSHIPS OF GEESE ON THE
EASTERN COPPER RIVER DELTA, ALASKA

A
THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By
James S. Hawkings, B. S.

Fairbanks, Alaska

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ABSTRACT

Migration and staging of geese were studied on the eastern Copper River Delta, Alaska, from 1978 to 1980. Spring migration occurred from mid-April to mid-May, and autumn migration from mid-August to at least mid-October. Branta canadensis taverneri and B. c. occidentalis were the most abundant taxa in both seasons. Saltmarsh was the most important spring and autumn habitat. Freshwater Meadows, which were Saltmarsh before the 2.5-m uplift during the 1964 Alaska Earthquake, are now characterized by tall vegetation, including shrubs, and were used intensively only by B. c. occidentalis during September. B. c. occidentalis ate many plants in autumn, most importantly Equisetum arvense, Triglochin palustris, and Carex lyngbyaei. Foods were predominantly leaves in August and seeds and roots in September. Visible migration was most correlated with fair weather and associated headwinds and crosswinds in spring, and with the most favorable southwest winds in autumn.

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INTRODUCTION

The Copper River Delta (CRD), located on the coast of south-central Alaska (Fig. 1), is an important breeding and migration area for waterfowl of the North American Pacific Flyway (King and Lensink 1971). In addition to being an "island" of suitable wetland habitat along the otherwise inhospitable rocky shorelines of the Gulf of Alaska and Prince William Sound, the Copper and adjacent Bering River Delta system (C-BRD system) lie along a natural migration corridor for millions of waterbirds (Isleib and Kessel 1973; Isleib 1977, 1979; Senner 1977, 1979). This corridor lies between high, rugged, glacier-studded mountain ranges inland, and the waters of the Gulf of Alaska. There are few wetlands comparable to the C-BRD system along this corridor between Puget Sound and the Yukon-Kuskokwim Delta. The most notable of these are the Fraser and Skagit Deltas in southern British Columbia and northern Washington, the Stikine Delta in southeastern Alaska, and the marshes and mudflats of Cook Inlet.

Geese are a significant component of both spring and autumn migration in the C-BRD system. At least nine taxa have occurred in migration, and six of these are common or abundant (Isleib and Kessel 1973, Isleib 1977): dusky Canada goose (Branta canadensis occidentalis), lesser Canada goose (B. c. parvipes), Taverner's Canada goose (B. c. taverneri), cackling goose (B. c. minima), white-fronted goose (Anser albifrons), and lesser snow goose (Chen caerulescens caerulescens). Of the remaining three taxa, black brant

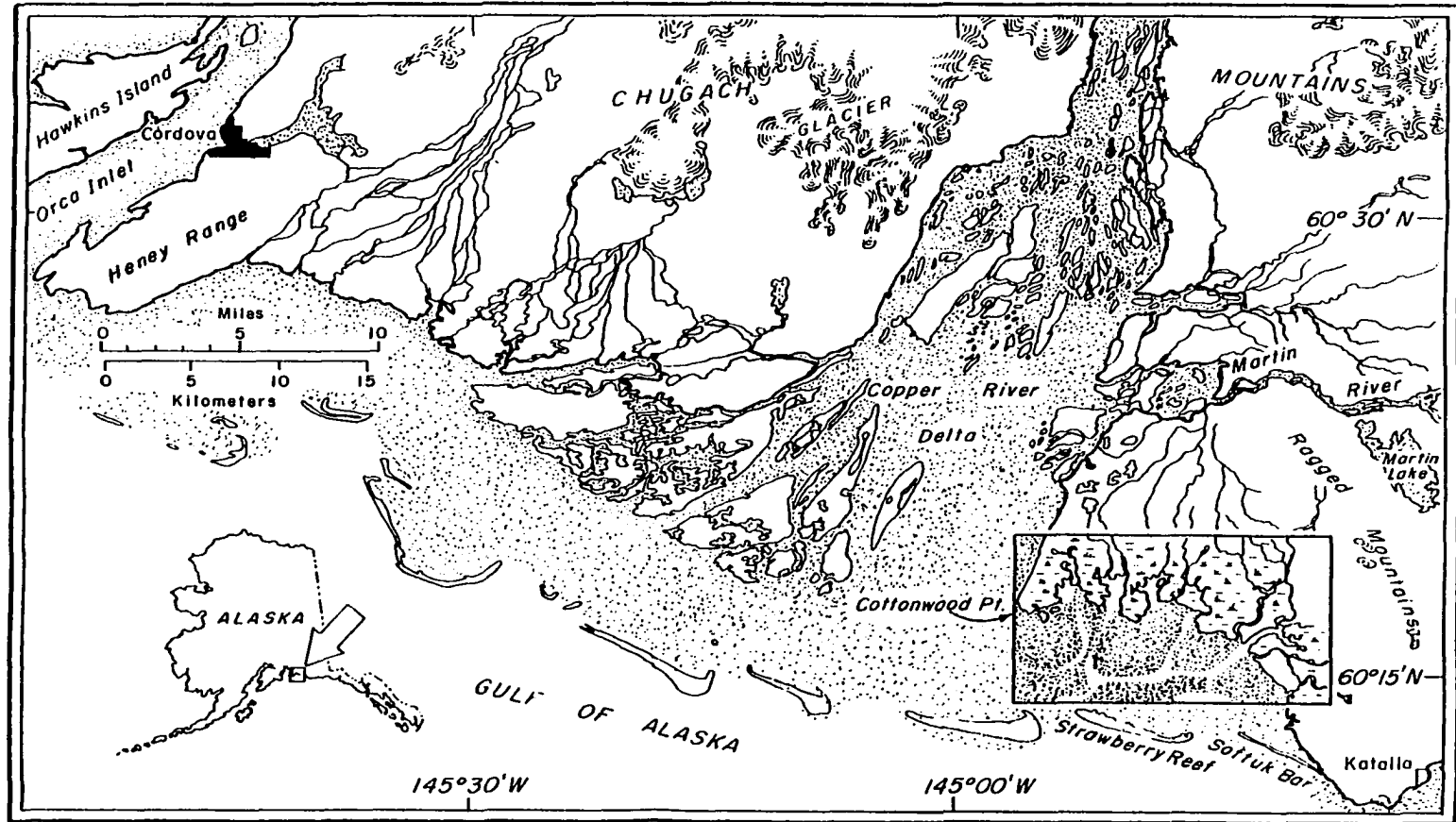


Figure 1. Location of the Copper River Delta, Alaska. Eastern Copper River Delta is indicated by the box. Western Copper River Delta lies between the Copper River and Heney Range.

(Branta bernicla nigricans) are fairly common, emperor geese (Philacte canagica) rare, and Aleutian Canada geese (B. c. leucopareia) known only from a few records. Virtually the entire population of the dusky Canada goose, which has fluctuated between 15,000 and 26,000 birds in recent years (Timm 1980), nests on the marshes of the western portion of the Copper River Delta (WCRD).

The most notable concentrations of geese using the C-BRD system during migration have been comprised of up to 100,000 white-fronted geese in early September (Gabrielson and Lincoln 1959, Isleib and Kessel 1973), but local residents tell of the regular gathering of "thousands" of white-fronted, snow, and Canada geese, particularly in the autumn. The eastern portion of the Copper River Delta (ECRD, Fig. 1) was a traditional autumn staging area for snow, dusky Canada, and white-fronted geese, and for sandhill cranes (Grus canadensis) within the C-BRD system according to Isleib and Kessel (1973) and local residents. A "staging area" is here defined as a particular location regularly used by a species in preparation for the next phase of its life cycle. This could involve physiological preparation or simply waiting for appropriate conditions.

The Good Friday earthquake of 27 March, 1964 dramatically altered habitats of the C-BRD system. The area was uplifted between 1.8 and 3 m, sufficient to raise the extensive saltmarsh above tidal influence and initiate drastic successional changes in vegetation (Reimnitz and Marshall 1965, Reimnitz 1972, Plafker 1969, Crow 1971). These saltmarshes were the major habitat used by migrating geese in

the system. Most of the saltmarshes of nearby Cook Inlet subsided 0-1.3 m, and were much less affected.

The present study was conducted to:

1. Determine present patterns of goose migration through the C-BRD system,
2. Determine the relationships between weather and goose migration patterns through the C-BRD system,
3. Determine patterns of habitat use and describe food habits of geese using the ECRD, and
4. Assess the importance of the C-BRD system as a migration area for geese.

STUDY AREA

The Copper River Delta ($60^{\circ}10'$ - $60^{\circ}25'$ N; $144^{\circ}35'$ - $145^{\circ}00'$ W) is a broad, elongate prism of sediment extending over 80 km along the coast of southcentral Alaska just east of Prince William Sound (Fig. 1). The Bering River Delta lies about 10 km to the east and extends another 23 km. Collectively, these deltaic systems comprise several thousand square km of barrier islands and spits, intertidal mud and sand flats, saltmarsh, and freshwater marsh. The C-BRD system is surrounded by rugged mountains and glaciers which typify most of the North Pacific coast between the Alaska Peninsula and southern British Columbia.

The Copper River Delta is unique owing to (1) the large volume of sediment supplied by the Copper River, (2) the extremely high energy of the adjacent marine environment, and (3) the tectonic instability of the coast (Galloway 1976). The Copper River transports 1/4 as much sediment as the Mississippi River, with only 1/6 the discharge. Westerly longshore currents and storm swells from the southeast combine to transport most of this sediment to the west, where it is deposited as far away as Orca Inlet and Prince William Sound. Sand predominates surface sediments in the western half of the Delta, whereas mud is found over most of the ECRD and at the extreme western end adjacent to the Heney Range (Galloway 1976).

The region has a long history of seismic activity as indicated by two buried forest horizons beneath the pre-earthquake saltmarsh;

these are dated at about 750 and 1,700 years before the present (Reimnitz 1972).

The climate of the area is maritime, characterized by relatively warm winters and cool summers (Rosenberg 1972). Mean annual precipitation at the Cordova airport on the WCRD is about 205 cm, but Cordova, located immediately northwest of the CRD in the fringe of the coastal mountains, receives about 300 cm (Isleib and Kessel 1973:7). September and October are the wettest months and June the driest. Precipitation and temperatures during this study are given in Table 1. High winds (50-100 km/h) from the E and SE are common during the autumn, winter, and early spring, associated with cyclonic storms moving eastward across the Gulf of Alaska. Tidal ranges in the C-BRD area average 3.8 m, with a maximum of about 5.6 m during spring tides (Brower et al. 1977).

The North Gulf Coast of Alaska and its avifauna were described in detail by Isleib and Kessel (1973). Studies of birds in the C-BRD system have been conducted by Hansen et al. (1971), Bromley (1976), Senner (1977, 1979), Holtan (1980), Mickelson et al. (1980), Smith (1980), Murphy (1981), and Herter (1982).

Table 1. Precipitation and temperatures recorded at the Cordova, Alaska, airport during spring and autumn migration watches in 1978 and 1979, and autumn of 1980.

| Year | Period | Precipitation | | Temperature ($^{\circ}$ C) | |
|--------|------------------|---------------|-----------|-----------------------------|-----------------------|
| | | Total (mm) | % of days | mean daily max. | mean daily min. |
| SPRING | | | | | |
| 1978 | 23-30 April | 57.9 | 88 | 8.9 | 1.6 |
| 1979 | 16-30 April | 4.6 | 33 | 10.0 | -1.6 |
| 1978 | 1-16 May | 37.6 | 81 | 11.6 | 2.8 |
| 1979 | 1-15 May | 73.4 | 93 | 10.0 | 2.2 |
| AUTUMN | | | | | |
| 1978 | 9-15 Aug. | 23.1 | 86 | 16.6 | 8.9 |
| 1979 | 6-15 Aug. | 132.6 | 100 | 15.0 | 10.6 |
| 1978 | 16-31 Aug. | 37.8 | 56 | 18.9 | 5.0 |
| 1979 | 16-31 Aug. | 101.6 | 56 | 17.2 | 7.2 |
| 1980 | 23 Aug. -4 Sept. | 23.9 | 54 | 17.8 | 3.9 |
| 1978 | 1-15 Sept. | 303.8 | 60 | 15.0 | 7.8 |
| 1979 | 1-15 Sept. | 127.8 | 66 | 18.3 | 6.1 |
| 1978 | 16-30 Sept. | 66.5 | 60 | 13.3 | 0.6 |
| 1979 | 16-30 Sept. | 204.5 | 93 | 11.1 | 6.1 |
| 1978 | 1-16 Oct. | 245.4 | 94 | 9.4 | 3.9 |
| 1979 | 1-21 Oct. | 311.4 | 81 | 9.4 | 3.3 |

METHODS

The eastern portion of the Copper River Delta (Fig. 2), lying between the 8 km-wide main channel of the Copper River and the Ragged Mountains, was the site of all field studies, which were conducted during 2 springs (23 April-16 May 1978; 15 April-15 May 1979), and 3 autumns (1 August-16 October 1978; 4 August-21 October 1979; 19 August-4 September 1980). Studies of sandhill cranes were carried out on the ECRD during 17 April-30 May and 17 August-15 October 1980, and 27 August-28 September 1981 (see Herter 1982). Some goose observations from these periods are also incorporated.

I. MIGRATION WATCHES

The basis for all migration watches, both spring and autumn, was a line directed north-south through the field camp at the mouth of Little River Slough (Fig. 2). All watches were conducted from a 4 m-high observation tower located at the field camp. Observers used binoculars and a 15-60x zoom telescope to monitor the passage of birds in both directions as far as possible along this line. In spring a minimum of two observers looking in opposite directions participated in each count; during the peak of migration there were at least three and often four observers, with one person serving exclusively as recorder. In the autumn most of the watches were conducted by a single person (usually myself) scanning both

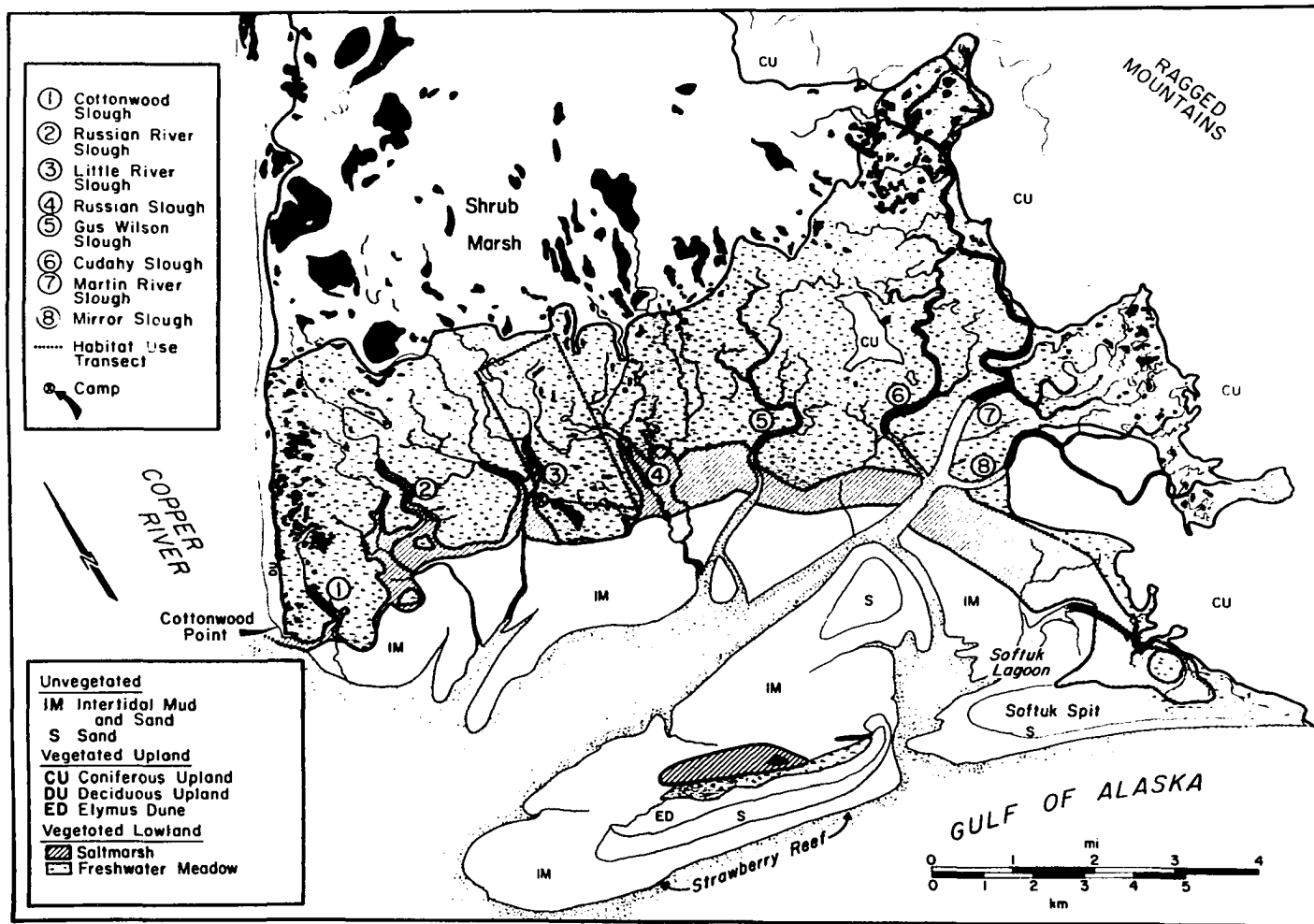


Figure 2. Habitat map of the eastern Copper River Delta, Alaska, showing locations of field camp and Freshwater Meadow habitat use transect.

directions alternately.

In the spring, migration watches were of 15 minutes duration, and were spaced at 2-h intervals approximately from dawn to dusk (0500 to 1900 local time). In the autumn a similar schedule was maintained (0700 to 1900; later 0700 to 1700) as much as possible. In autumn I increased observation time to provide more observations of less common species such as white-fronted geese. In 1978 this additional time was usually in 1/2-h periods, and in 1979 usually 1-h periods, spaced irregularly throughout the day. The timing of these additional watches varied according to my other activities, but was not affected by changes in migration intensity within any particular day. On some days when activity appeared intense early in the morning, I increased the amount of observation time throughout the day.

For each flock crossing the north-south line, I recorded the taxon as precisely as possible, flock size, direction, and altitude. For both spring and autumn, I treated the original 15-minute watches as an unbiased sample of each day's migration. Within each watch, movements were totalled separately for each taxon, and for all geese. I then estimated the mean rate and total volume of eastward, westward, and, by subtraction, net movement, for each day (12 h only) and for the entire season. I initially divided the additional autumn observation time into 15-minute segments, and treated them as independent units. However, because of possible serial correlation among consecutive segments, I re-analyzed the 1979 data using a ratio

estimator (Cochran 1953), which allowed the use of variable-length, more independent observation periods. This also resulted in fewer zero values due to the longer periods. The results of both methods were similar (Appendix 1B), so I concluded that it was unnecessary to re-analyze the autumn 1978 data. I used only the ratio estimator for the autumn 1980 data.

I also maintained daily checklists of the total numbers of each taxon seen; including those seen (1) during migration watches, and (2) during other activities; these proved more useful than the migration watches alone for documenting the phenology of spring migration for the less abundant taxa such as cackling, snow, and white-fronted geese.

II. IDENTIFICATION OF SUBSPECIES

For Branta canadensis subspecies, I used the classification of Bellrose (1976), which is consistent with other recent studies in the Pacific Flyway (Johnson et al. 1979, Simpson and Jarvis 1979). For A. albifrons, I used the nomenclature of Krogman (1979).

In the field I used the criteria of size, coloration, and voice to distinguish among Branta canadensis subspecies: occidentalis (dusky), taverneri (Taverner`s), and minima (cackling). Large numbers of occidentalis have been neck-collared in recent years on their breeding grounds on the WCRD, and these collars were also helpful in confirming identifications. I tentatively identified the two

subspecies of white-fronted geese by differences in size and coloration. Tule geese (A. a. gambelli) are distinctly larger and darker, especially in the head and neck region, than are the more abundant Pacific white-fronted geese (A. a. frontalis). Birds collected for food habits studies (see below) or shot by hunters were identified using measurements and weights (Johnson et al. [1979] for B. c. canadensis; Krogman [1979] for A. albifrons), and coloration.

III. HABITAT RELATIONSHIPS

A. Habitat Classification

I mapped habitats on the ECRD using (1) 1:15,840 scale 1974 color aerial photography, (2) 1:130,000 scale 1976 infrared aerial photography, and (3) a previous vegetation map of the area and an accompanying report (Scheierl and Meyer 1977). I used my own ground and aerial observations to determine the extent and nature of pioneering vegetation in the Saltmarsh, which was impossible to delineate on either the 1974 or 1976 photography. Plant nomenclature follows Hulten (1968).

I classified seven habitats on the ECRD study area: Intertidal Mud and Sand, Saltmarsh, Freshwater Meadow, Shrub Marsh, Coniferous Upland, and Elymus Dune. These are described in detail and related to the classification of Cowardin et al. (1979) in Appendix II. Geese almost exclusively used the two vegetated wetland types, Saltmarsh

and Freshwater Meadow. Saltmarsh areas are tidally influenced, presently have relatively short, sparse vegetation, and are virtually free of shrubs. The Freshwater Meadow is above even the highest spring tides; it has 100% vegetative cover, a wide variety of plants, and abundant shrubs, many of which exceed 4 m in height.

B. Habitat Use

i. Spring

Most of my observations of spring habitat use are from 1979 because I did not arrive at the field camp until 5 May in 1978. In 1979 these observations were made opportunistically from the observation tower at the field camp, usually before or after the 15-minute migration watches. I also made observations on the ground within a 2-km radius of the camp.

ii. Autumn

During autumn I conducted separate censuses of geese in each of the two most important habitats (Saltmarsh, Freshwater Meadow). In all three years, I regularly (3-8/day) counted all geese using the Saltmarsh at the mouth of Little River Slough (Fig. 2), and used the mean count of each taxon over each day's censuses as an index of use.

From the observation tower it was impossible to see geese on the

ground in the Freshwater Meadow owing to the height of shrubs and grasses. To determine use of this habitat I established a 9.5-km line transect which I walked at 2-5 day intervals from 7 August to 20 October in 1979 and 19 August to 3 September in 1980. For each flock I observed on the ground or flushed along this transect I recorded flock size, taxon, and perpendicular distance to the line. I then used Emlen's (1977) cue-attenuation method to determine the effective width of the transect, and included only those observations falling within this effective width.

C. Succession

I determined the extent and nature of pre-earthquake vegetation on the ECRD study area by (1) examining drainage and vegetation patterns in both pre-earthquake (1958) and recent (1974, 1976) aerial photography of the ECRD; and (2) comparing the present and past condition of the ECRD to that of the WCRD and the saltmarshes of upper Cook Inlet.

IV. FOOD HABITS

A. Stomach Collection and Analysis

Stomachs were obtained from geese (1) collected opportunistically by myself and other biologists on the ECRD, and (2)

shot by recreational hunters. Owing to the tall vegetation and constraints imposed by other activities, it was impossible to ensure that birds were feeding immediately prior to collection; consequently, some had empty proventriculi.

Only food contents of the esophagus and proventriculus were used in the analysis in order to avoid biases caused by differential digestion rates of foods found in the gizzard. Within each sample, food items were sorted by taxon as specifically as possible using a reference collection and Hulten (1968), and further classified as leaf (including stem or shoot), seed, or root material. The proportion of each item in the entire contents of the sample was then visually estimated on a volumetric basis. To demonstrate changes with time, and eliminate biases caused by unequal sample sizes through the autumn, I divided the autumn into one 3-week and three 2-week collection periods; mean proportions (aggregate or mean percent volume) and the percent of birds in which each food item occurred (percent frequency of occurrence) were then calculated for each period (Swanson et al. 1974).

B. Vegetation Sampling

Vegetation was sampled along six N-S transects spaced at 1.6-km intervals from Cottonwood Slough to Gus Wilson Slough (Fig. 2). Each extended from the Freshwater Meadow/Shrub Marsh interface at the N to the seaward limit of Saltmarsh vegetation in the S. With a randomly

selected starting point, one 1 X 1-m plot was examined at 200-m intervals along these transects. Each plot was subdivided into four equal quadrats within which the percent cover of each species was visually estimated. These figures were added to give a total for each species within the plot. Sampling was done from 19 July to 12 August 1979. A total of 129 plots were sampled in the Freshwater Meadow and 24 in the Saltmarsh. Both relative cover and percent frequency of occurrence of plant species were calculated over all the plots in each habitat:

$$\text{relative cover species } i = 100 \left(\frac{\sum_{j=1}^N c_{ij}}{\sum_{i=1}^k \sum_{j=1}^N c_{ij}} \right)$$

$$\text{percent frequency of occurrence species } i = 100 n_i / N$$

where c_{ij} = % coverage for i th species in j th plot

k = total number of plant species

n = number of plots in which species i is present

N = total number of plots sampled

V. THE INFLUENCE OF WEATHER ON MIGRATION

Weather can affect migration watches by influencing (1) the number of birds aloft, and (2) the ability of observers to see them. The second effect can be manifested in changes in the route or

altitude of migration, or in changes in sightability caused by obstructions such as clouds, fog, precipitation, etc. The North Gulf Coast of Alaska in the area of the CRD is a particularly difficult area for which to interpret migration watch data because it probably acts as a "leading line" along which migrants concentrate under certain weather conditions (Alerstam and Pettersson 1977, Alerstam 1978).

Because of these biases there is no definitive way to relate the amount of visible migration to the amount of actual migration without measuring both independently (e.g. using radar). If the relationships between the visible migration and weather can be elucidated, however, specific hypotheses about the true migration can be formulated. I examined these relationships for spring and autumn migration using synoptic weather, individual original weather variables, and latent variables (factors) representing combinations of the original variables.

A. Choice of Migration Periods

I restricted most analyses to those periods during spring and autumn in which there was evidence of substantial migration either during this study (see Results), or based on previous knowledge. I used the entire migration watch period in spring, but in autumn only the month of October consistently had days of heavy migration. There was a smaller peak in autumn migration during late August/early

September composed of dusky Canada and white-fronted geese, but since most of the former appeared to be involved in only short, local movements, and relatively few flocks of the latter were observed, I felt that the migration watches would not necessarily reflect daily changes due to the weather. There was also relatively little variation in weather conditions at this time compared to later in the autumn. Migration was only examined in relation to synoptic weather conditions during this period.

B. Synoptic Weather Systems

To determine relationships between synoptic weather and visible migration, I examined daily surface weather maps, and plotted the location of the Copper River Delta relative to the predominant high and low pressure centers on a single generalized weather map (cf. Blokpoel and Gauthier 1980) for each season.

C. Individual Weather Variables

Most weather variables chosen for analyses (see Table 7) were measured at the Cordova airport, 21 km E of Cordova on the WCRD. Upper air and surface winds were also obtained from Yakutat and Anchorage, since (1) no upper air wind measurements are made at Cordova, and (2) geese passing the ECRD might have initiated flights from the Yakutat area in spring and upper Cook Inlet in autumn.

Thirty-four wind variables were considered, of which 22 were wind components and temporal changes in them. The remaining 12 were expected groundspeeds derived from these winds (Alerstam 1978). Winds were resolved into headwind-tailwind and crosswind components based on the expected preferred track of migrants in spring (310 degrees true N) and autumn (130 degrees true N). These components thus approximate NW-SE and SW-NE. The 11 other weather variables measured cloudiness, visibility, precipitation, temperature, and pressure at the Cordova airport. Two temporal variables were considered in later regression analyses to account for the expected increase, peak, and decline in actual migration with time.

To meet the normality assumptions of correlation, regression, and factor analysis, some variables were transformed. Since migration volume itself was highly skewed, the logarithm of (migration volume + 10) was used, the 10 added to avoid problems caused by zero counts; ten, rather than one, was used to further reduce skewness in the resulting logarithm.

D. Multiple Regression Analysis

Regression analyses were carried out in a forward stepwise manner using a BMDP2R computer program (Dixon and Brown 1979) with an F-to-enter of 2.0, and a maximum of 5 steps allowed. Bivariate correlations were obtained from the correlation matrix provided by BMDP2R. Missing values necessitated the elimination of many wind

variables from the analysis, particularly in spring. Twenty-two weather variables were used in the spring analysis, and 45 in autumn. Plots of residuals were examined for abnormal patterns (Draper and Smith 1966).

E. Factor Analysis

Since an independent variable necessary for a predictive model of visible migration based on weather, i.e. the number of birds ready to migrate, was unknown during most of the study, and could only be grossly accounted for during a short period in spring (see Results), I attempted to characterize weather conditions on days of heaviest visible migration during spring and late autumn, and ignored days on which there was little or no migration. I did this by first identifying hypothetical weather variables (factors), each of which represented a different group of inter-correlated original weather variables. Application of this procedure (Factor Analysis) to daily weather data for the entire spring and late autumn periods reduced approximately 20 highly intercorrelated weather variables to six or seven relatively uncorrelated "factors", which could then be related to migration volume. I then plotted daily migration volume against these factors to determine which were most useful in characterizing days of heavy migration, and interpreted the results by relating the most useful factors back to their constituent original variables.

As in the regression analyses, missing values necessitated the

elimination of some variables to maximize the number of usable cases. Nineteen variables were used in the spring and 25 in autumn. Analyses were performed using a BMDP4M computer program (Dixon and Brown 1979). Initial factor extraction was by Principal Components. Those Principal Components with eigenvalues greater than 1.0 were then transformed by means of a non-orthogonal ("Direct Quartimin") rotation to simplify the pattern of factor loadings (correlations of factors with the original variables). Non-orthogonal rotation allows factors to be oriented in space such that they are no longer uncorrelated with one another, but it is the recommended procedure for interpretive purposes where orthogonal factors are not required and variables do not tend to cluster in an orderly fashion on the initial factors (Frayne and Hill 1976). This transformation seeks to express each original variable in terms of a minimum number of factors by maximizing the variance of each original variable's loadings across all the factors. Thus each variable will tend to be highly correlated with a minimum number of factors (ideally one) and uncorrelated with the remainder (Frayne and Hill 1976).

F. Statistical Significance of Results

Statistical significance is coded throughout as: (*) if $0.1 \geq P > 0.05$, * if $0.05 \geq P > 0.01$, ** if $0.01 \geq P > 0.001$, *** if $0.001 \geq P$. In regression models "apparent significance" levels are presented, although these are gross overestimates of actual significance values

because of the large predictor variables:cases ratios (spring 22:51, April only 24:21, autumn 45:31), and the criteria used for inclusion of predictor variables (Forsythe 1979).

RESULTS

I. IDENTIFICATION OF SUBSPECIES

In 1978 subspecies of Canada geese were not differentiated until the passage of Branta canadensis minima in May, whereas during the spring of 1979 I was able to separate subspecies in many instances. I was never able to make positive identifications of lesser Canada geese (B. c. parvipes) among flocks of B. c. taverneri, although several thousand of the former undoubtedly passed through in both 1978 and 1979. The breeding range of parvipes is not clearly delineated in Alaska, but it is thought to be the subspecies breeding in upper Cook Inlet, where about 2,000 nest (Timm and Sellers 1980), and in many areas of the Interior. Several authorities (see Johnson et al. 1979) agree that taverneri is generally a tundra breeder, while parvipes is found in forested areas. The morphological variability of parvipes throughout its range in Alaska is unknown, but Johnson et al. (1979) could not reliably separate those breeding in Cook Inlet from taverneri, even using multivariate analysis. They also encountered difficulty separating parvipes from occidentalis. Consideration of coloration would probably refine the separation of these three taxa, but until it is measured quantitatively and objectively, especially in the case of taverneri vs. parvipes, coloration remains an unreliable parameter to use.

I will refer to all medium-sized Canada geese with coloration

lighter than occidentalis as taverneri because (1) these two taxa are easily separable in the field using voice, size, and/or coloration; (2) taverneri is far more abundant than parvipes on the Pacific Coast (most parvipes migrate through the interior regions of British Columbia, Yukon Territories, and Alaska [see Myres and Cunnings 1971]); (3) most of the medium-sized birds I observed during the study were markedly smaller than occidentalis (parvipes is only slightly smaller); and (4) all of approximately 10 "lessers" I examined in the hand were taverneri.

There is evidence that parvipes passes through the CRD. D. Herter (pers. comm.) observed two sizes of "lessers" in a single flock on the ECRD in late September 1980, and local hunters in the area claim there are two sizes present in October.

II. TIMING, AMOUNT, AND ROUTES OF MIGRATION

A. Nocturnal Migration

Nocturnal migration cannot be measured by conventional migration watches, and no attempt was made to quantify it in this study. Substantial migration, mostly of B. c. taverneri (identified by voice), did occur during the nights of 14/15, 15/16, and 21/22 April and 13/14 October in 1979, and on 10/11 and 13/14 October in 1978. Records of nocturnal migration were not kept during spring 1978. Isleib (1977) also noted night passages of Canada geese during the

night on 22/23, 23/24, and 24/25 April 1975, and 22/23 April 1976, during a two-year study of spring migration at the eastern entrance to Prince William Sound (55 km E of the ECRD). He stated that the major autumn migration of Canada geese from Cook Inlet via Prince William Sound usually passes the CRD area at night.

B. Data Presentation

Migration through the ECRD is described here in three ways. First, total daily rates of migration calculated from migration watches are depicted (Figs. 3, 4), and are subdivided by species as much as possible. These provide an overview of the timing within each autumn and spring migration and also serve as a basis for comparison among years.

Secondly, from the same data, estimates of the total volume of migration are presented for (1) all geese as a whole, and (2) white-fronted and snow geese (Table 2). Estimates for Canada geese are not presented because subspecies were too infrequently identifiable during migration watches in spring and late autumn. Although the total estimates of migration volume, and especially those for white-fronted and snow geese, are underestimates, they are useful as a basis for comparing changes in the future.

Finally, uniformly fair weather persisting throughout the last two weeks of April in 1979 provided a unique opportunity to make supplemental observations during that spring. These data (Fig. 5)

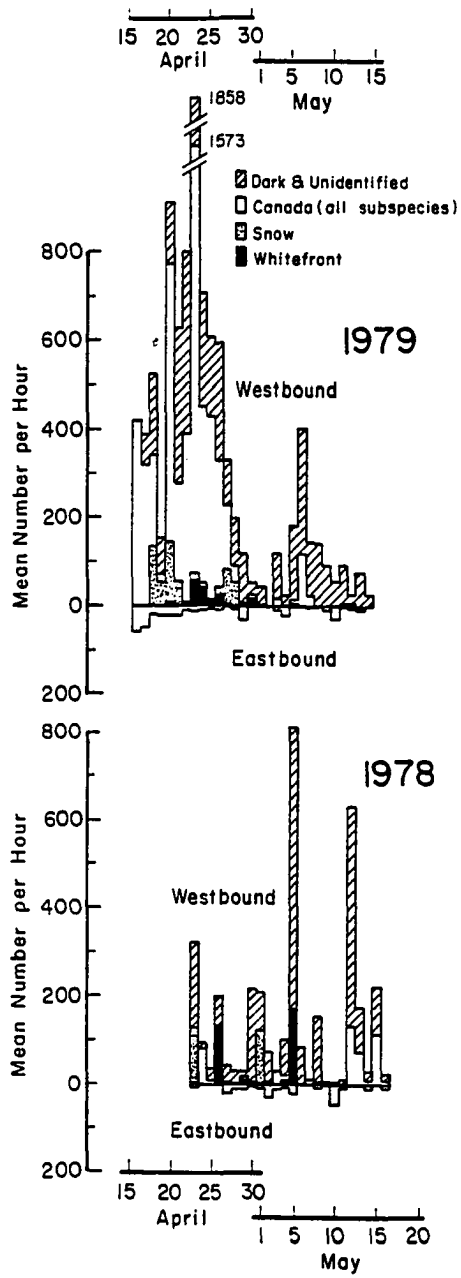


Figure 3. Rates of visible spring goose migration through the eastern Copper River Delta, Alaska, determined by migration watches in 1978 and 1979. Gaps indicate days with no migration watches.

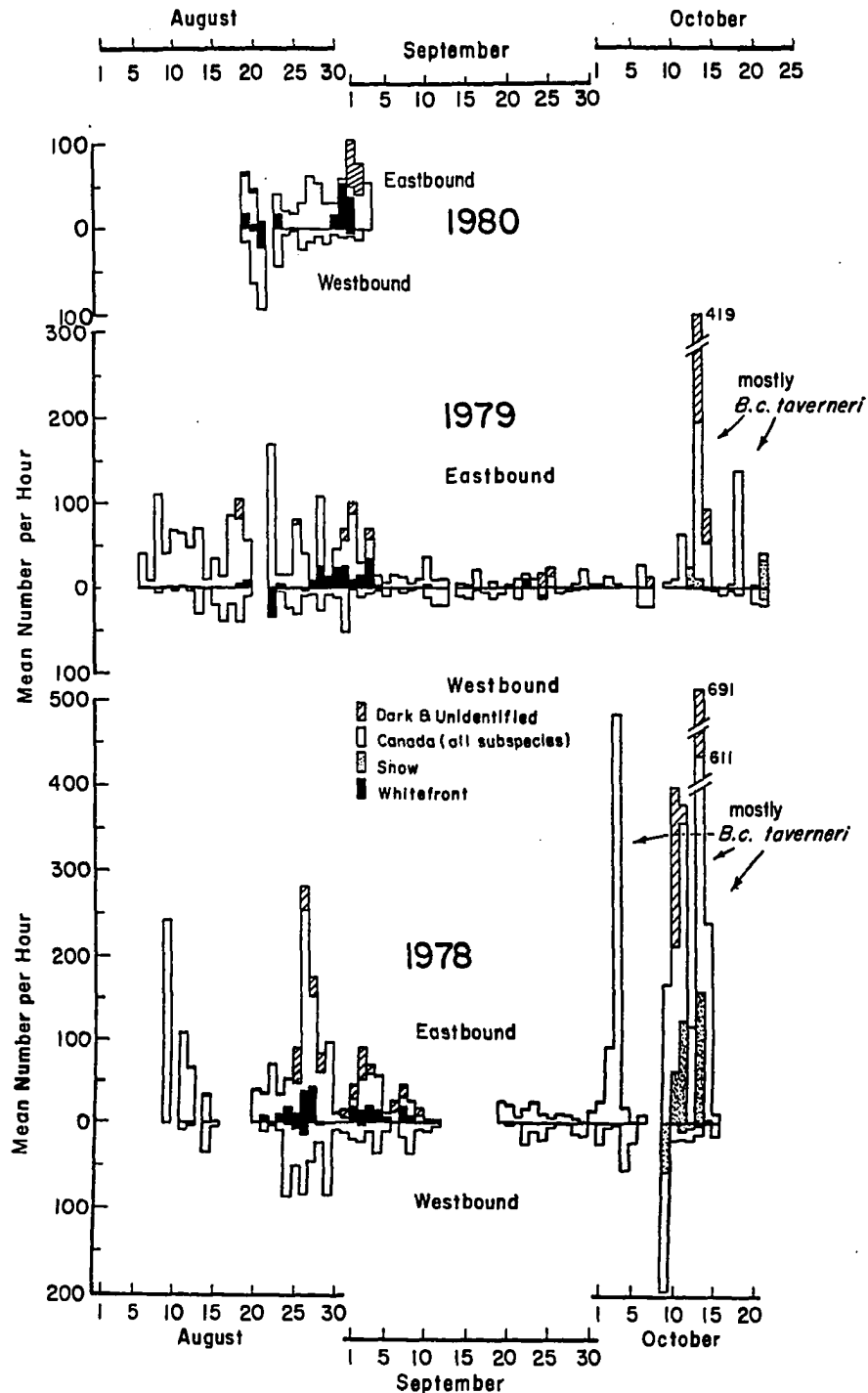


Figure 4. Rates of visible goose migration through the eastern Copper River Delta, Alaska, determined by migration watches in autumn 1978, 1979, and 1980. Gaps indicate missing data. Virtually no migration occurred on 7-8 October 1978 due to strong winds, which also prevented migration watches.

Table 2. Estimates of the total volume of visible goose migration through the eastern Copper River Delta, Alaska in 1978, 1979, and 1980, based on migration watches. Estimates are for daylight hours only, based on 12 h daylight/day.

| | 1978 | | 1979 | | 1980 | |
|---|----------------------|--------|----------------------|--------|--------------------|-------|
| | Number of Geese | SE | Number of Geese | SE | Number of Geese | SE |
| A. All Taxa | | | | | | |
| SPRING | | | | | | |
| 16-19 April | | | 16,236 | 7,560 | | |
| 20-30 April | | | 80,028 | 37,860 | | |
| 23-30 April | 11,160 | 7,356 | 52,968 | 26,976 | | |
| 1-15 May | 28,836 | 16,248 | 17,124 | 10,920 | | |
| Total | 40,236 | 23,760 | 113,388 | 56,340 | | |
| AUTUMN | | | | | | |
| 6 August - 3 September | | | 13,656 ^b | 8,280 | | |
| 9 August - 3 September | 13,336 ^a | 9,960 | 11,808 ^b | 7,344 | | |
| 19 August - 3 September | 8,540 | 6,864 | 7,176 ^d | 4,164 | 4,404 | 5,688 |
| 4-30 September | 1,608 ^c | 3,516 | 1,008 ^d | 2,484 | | |
| 1-15 October | 25,548 ^e | 15,276 | 7,212 ^e | 1,272 | | |
| 1-21 October | | | 8,808 ^e | 3,036 | | |
| Total | 40,492 | 30,636 | 23,472 | 13,800 | | |
| B. <u>Anser albifrons</u> | | | | | | |
| SPRING | | | | | | |
| 16-22 April | | | 240 | 168 | | |
| 23 April - 15 May | 3,744 | 2,976 | 1,944 | 1,260 | | |
| Total | 3,744 | 2,976 | 2,184 | 1,428 | | |
| AUTUMN | | | | | | |
| Total | 2,148 ^{ace} | 1,896 | 1,908 ^{bde} | 1,308 | 1,440 ^f | 1,500 |
| C. <u>Chen caerulescens</u> | | | | | | |
| SPRING | | | | | | |
| 16-22 April | | | 4,608 | 3,048 | | |
| 23 April - 15 May | 3,384 | 2,976 | 2,292 | 1,812 | | |
| Total | 3,384 | 2,976 | 6,900 | 4,860 | | |
| AUTUMN | | | | | | |
| Total | 3,228 ^{ace} | 3,048 | 528 ^{bde} | 636 | | |
| Notes: ^a no data 10,12,16-19 August. ^b no data 20,21 August. ^c no data 12-18 September. ^d no data 13 September. ^e no data 8 October. ^f 19 August - 3 September only. | | | | | | |

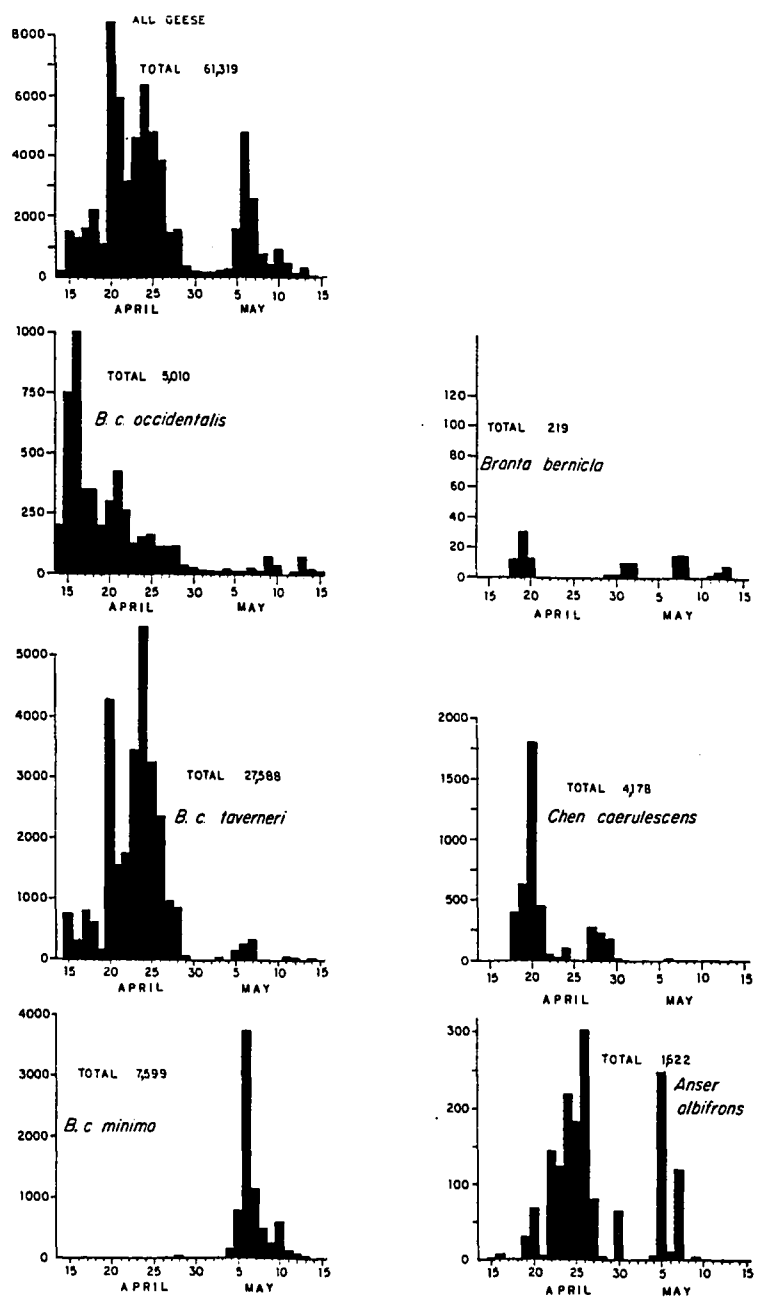


Figure 5. Daily totals of geese observed on the eastern Copper River Delta during spring 1979. Both migration watch and supplemental observations are included. Substantial numbers of "dark" and "unidentified" geese are included under "ALL GEESE".

show the phenology of the migrations of Canada goose subspecies and indicate their relative abundance.

C. Taxon Accounts

i. Dusky Canada Goose (Branta canadensis occidentalis)

a. Spring

B. c. occidentalis was the earliest spring migrant on the study area (Figs. 3, 5). In 1978 spring was exceptionally early and migration of this subspecies was practically complete when migration watches began on 23 April. In 1979 spring was slightly later, but some dusky were already on the WCRD when migration watches began on 16 April. The last major movement in 1979 occurred on 21 April. Bromley (pers. comm.) estimated peak arrival of dusky Canada geese on their WCRD breeding grounds as 17 and 18 April in both years.

The small size of occidentalis flocks in spring (Table 3) is probably due to the proximity of the ECRD to the breeding grounds of the majority of the population. An estimated 200-300 pairs actually nest on the ECRD (Mickelson et al. 1980). Many passing birds were already paired (i.e. flock size of two), and feeding flocks were usually loosely structured with each pair or apparent family group maintaining a distance from others.

In contrast to their behavior in the autumn, a number of spring

Table 3. Flock sizes of geese observed during spring and autumn migration watches on the eastern Copper River Delta, Alaska.

| Taxon | Year | SPRING | | | | AUTUMN | | | |
|-------------------------------------|-------------------|--------|------|----|--------|--------|------|----|--------------------|
| | | N | Mean | SD | Range | N | Mean | SD | Range |
| <u>Chen caerulescens</u> | 1978 | 7 | 72 | 65 | 2-170 | 29 | 39 | 48 | 1-210 |
| | 1979 | 33 | 33 | 33 | 2-125 | 6 | 42 | 37 | 5-90 |
| <u>Anser albifrons</u> | 1978 | 8 | 58 | 76 | 3-195 | 54 | 16 | 18 | 1-90 |
| | 1979 | 27 | 11 | 15 | 1-40 | 44 | 23 | 20 | 1-90 |
| | 1980 | 0 | | | | 23 | 38 | 60 | 1-300 ^c |
| <u>B. c. taverneri</u> ^a | 1978 ^b | 0 | | | | | | | |
| | 1979 | 118 | 43 | 58 | 1-400 | 22 | 20 | 41 | 1-180 |
| <u>B. c. occidentalis</u> | 1978 | 71 | 2 | 2 | 1-10 | 488 | 16 | 27 | 1-330 |
| | 1979 | 192 | 4 | 10 | 1-130 | 724 | 16 | 25 | 1-350 |
| | 1980 | 0 | | | | 189 | 16 | 15 | 1-115 |
| <u>B. c. minima</u> | 1978 | 10 | 68 | 61 | 18-200 | 0 | | | |
| | 1979 | 9 | 43 | 52 | 2-175 | 0 | | | |

Notes: ^a including small numbers of B. c. parvipes.

^b B. c. taverneri were not distinguished from other "unknown" Canada geese in 1978.

^c discounting 1 flock of 300, mean=26, SD=19, range=1-85.

migrants bypassed the ECRD without stopping. This was evident from flocks that passed the field camp at over 100 m and continued to the west past Cottonwood Dunes. Many others probably stayed for only a few hours, although two neck-collared birds remained for 5 and 7 days between 16 and 26 April 1979. These birds probably did not nest on the ECRD as neither was seen again during the summer.

b. Autumn

B. c. occidentalis was the first autumn migrant to appear and among the last to leave in both 1978 and 1979. No other Canada goose subspecies was present on the ECRD until at least mid-September, except for occasional individual Taverner's Canada geese. Since the breeding population on the ECRD was less than 300 pairs in both years, and there was little apparent increase in the population during an eastward molt migration ca. 20 June, it was relatively easy to detect the first influxes of migrants. In both 1978 and 1979 the first flocks capable of flight appeared during the first few days of August (slightly earlier in 1978 than 1979), at which time local ECRD breeders and their young were still flightless. By 5-7 August flocks were steadily moving east in short flights, and hundreds of birds could be found feeding in the larger expanses of Saltmarsh on the ECRD and Strawberry Reef Island.

In both years a similar pattern of movements occurred (Fig. 4). During August net migration was eastward, but movements were far less

directional than in spring. Movements all appeared to be local, actual migration being composed of a number of eastward hops. For example, most flocks passing or departing from Little River Slough landed again in the next large patch of Saltmarsh, about 2 km E. This pattern continued until 4-7 September, after which little net movement was discernable until a final exodus during October that partially coincided with the passage of B. c. *taverneri*.

I interpret this pattern as comprising the following events: (1) post-molting dispersal from breeding and molting areas to new feeding grounds, primarily to the east; (2) a staging period during which birds were fairly sedentary, feeding in Freshwater Meadow habitat; and (3) final exodus from the Copper River Delta of birds that staged there. Similar peaks in numbers of passing Canada geese at Yakutat during autumn 1980 (Petersen et al. 1981) suggest that this initial dispersal extends far down the Pacific coast. The final movement of *occidentalis* in October was difficult to quantify since viewing conditions were frequently too poor to distinguish between that subspecies and the more abundant *taverneri*. The best evidence of the final exodus was flocks of *occidentalis* occasionally observed moving east in October, whereas there was almost no discernable movement during the entire staging period in September. A slight increase in the number of *occidentalis* using the Saltmarsh from late September to mid-October and a decline in use of the Freshwater Meadow (see Habitat Use) also suggested that birds were becoming more transient, although this may have been partially due to the attraction of

occidentalis to flocks of taverneri in the Saltmarsh. A few occidentalis remained on the ECRD after field observations were terminated in both years.

The most intensive movement of occidentalis occurred in all three years during the initial post-molting dispersal in August and the first few days of September. In fact, the net eastward movement past Little River Slough during this time was about 10 times as large as during the remainder of September (Table 2). Thus, it seems that the great majority of occidentalis depart the CRD by 3 September, a conclusion corroborated by (1) the observations of local hunters, and (2) the results of aerial surveys conducted in autumn 1980 and 1981 by the Alaska Department of Fish and Game (Campbell et al. 1981). I estimate the population on the entire ECRD at any one time during the period mid-August to late September in both years at 2,000 to 3,000 geese.

Layover times of B. c. occidentalis on the ECRD were determined from a series of sightings of neck-collared individuals at Little River Slough (Fig. 6). Neck-collars were most easily read when birds were in the Saltmarsh at the mouth of Little River Slough. In the Freshwater Meadow, neck-collars were almost impossible to read due to the height of vegetation and wariness of the geese. Thus, after early September when most occidentalis had switched their feeding activities from the Saltmarsh to the Freshwater Meadow, I read few neck-collars even though there may have been similar numbers of neck-collared birds on the study area. Fewer birds frequented the

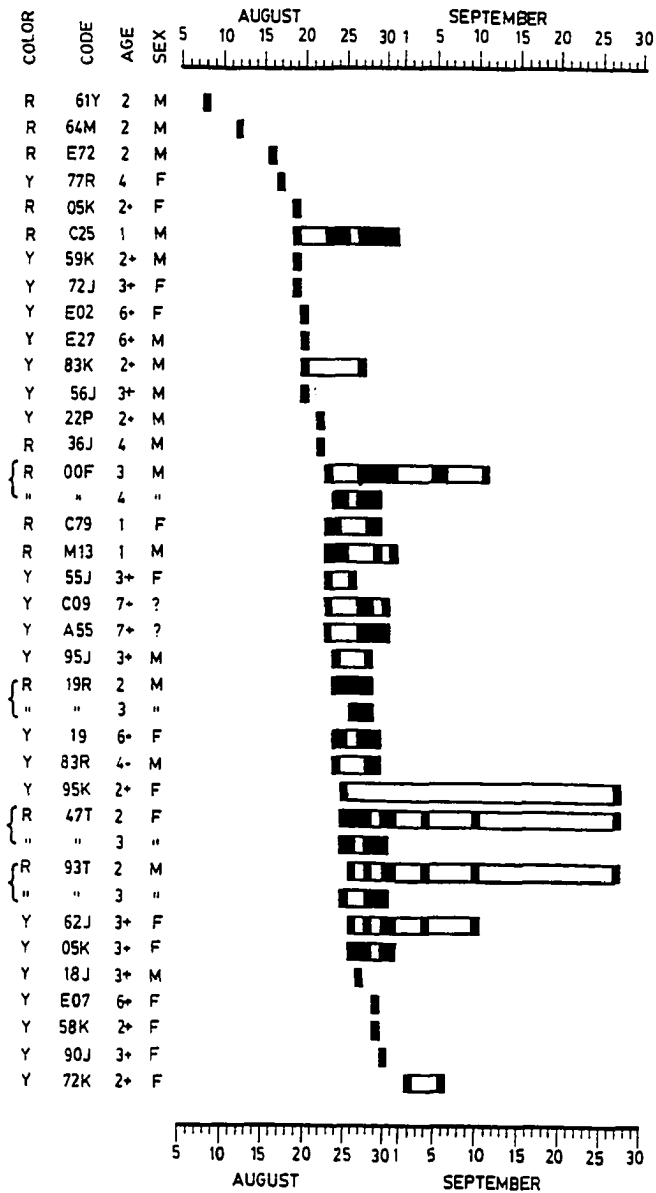


Figure 6. Minimum layover times of individual neck-collared dusky Canada geese on the eastern Copper River Delta, Alaska, during autumn 1979 and 1980. Solid segments are sightings. Brackets indicate individuals seen in both years.

Saltmarsh in late August of 1978 than 1979, possibly due to shorebird studies which were being conducted there in 1978 (Murphy 1981), in plain sight of geese flying over or on the ground in the Saltmarsh. As a result, only two collars were read in 1978.

Because collared birds were often present without their collars being read, the intervals between sightings of individuals are considered minimum times spent on the ECRD. In 1979 most collars were last read near the end of August, when the major habitat shift was occurring. Those read after 9 September were in small flocks briefly loafing or feeding in the Saltmarsh.

At least three collared birds had lengthy stays on the ECRD extending through the shift from one habitat to the other (Fig. 6). From these sightings and the relatively stable number of birds on the study area from late August to late September, I believe this lingering was typical of most of the adult non-breeders and failed-breeders that used the ECRD. Since none of the neck-collars read in 1979 were on juveniles (no neck-collaring was done in 1979) or adults with young, there is only circumstantial evidence (i.e. lack of visible migration during September) that layover times for family groups were comparable.

Neck-collar observations support the notion that individual dusky Canada geese have traditional autumn staging areas, as do other Canada geese (Raveling 1979; Zicus 1981). Some neck-collared individuals appeared in August and remained in the immediate area of Litte River Slough every day while other geese continued to pass in a

substantial eastward movement. In addition, four neck-collared individuals appeared and remained on the ECRD in both 1979 and 1980 (Fig. 6).

In both 1978 and 1979 adults unaccompanied by juveniles were the first arrivals on the ECRD in August (excepting the few local breeders, most of which were still flightless until near the middle of the month). Neck-collar sightings showed that these flocks comprised both yearlings and older unsuccessful nesters. I saw the first evidence of juveniles capable of flight during the second week of August in both 1978 and 1979. From early September through mid-October all age classes were present. In 1979 and 1980 there were far fewer juveniles than in 1978, reflecting extremely poor production (Timm 1980, D. Timm pers. comm.). In 1978, nine of 14 birds (72%) shot by hunters or collected for food habits studies were juveniles versus only 30 of 86 (35%) in 1979 ($\chi^2=3.22$, $0.1 > P > 0.05$).

ii. Taverner's Canada Goose (B. c. taverneri)

a. Spring

Taverner's Canada geese were the most abundant spring migrants through the ECRD. In 1979 the spring migration apparently began coincidentally with our arrival on the ECRD on 14 April and peaked from 20 to 26 April (Fig. 5). This is the normal peak of migration for this subspecies in the Cook Inlet and North Gulf Coast area

according to Isleib (1977). Ritchie et al. (1981) recorded peak numbers (9,000) moving through the Palmer area near Anchorage on 23 April 1980.

This subspecies occurred regularly in mixed flocks with other geese, whistling swans (Cygnus columbianus) and occasionally pintails (Anas acuta) or sandhill cranes. Flocks of taverneri tended to fly at higher altitudes and were larger than those of occidentalis (Table 3). Probably fewer than 10% of all flocks stopped on the ECRD. Of those that did, most departed again within several hours, and many alighted for only a few minutes. Frequently only part of a flock would land while the remainder continued west. The impression was one of a rapid turnover process, as each flock stopped no more than once on the ECRD.

b. Autumn

In both autumns the major visible passage of B. c. taverneri occurred en masse on a few favorable days between early and mid-October (Fig. 4). Isleib (1977) stated that the passage through Prince William Sound is from 15 September to 1 November with a peak around 10 October. In 1971 a single, massive migration occurred on 11 and 12 October, after three days of storms (J. Reynolds in litt.), and in 1980 there was only one movement, which occurred on 10 and 11 October (D. Herter pers. comm., D. Timm unpubl. data). In the two years of this study no substantial movements of this subspecies

occurred until October, although I observed small flocks in late September and single individuals as early as August. Some taverneri evidently migrate after mid-October in some years. For example, in 1978 there was "an exceptionally late major movement" of Canada geese along the coast between Cordova and Yakutat, and up to at least 20 km at sea, on 1-2 November (Gibson 1979). Local fisherman/hunter D. Curran (pers. comm.) has noted passages of "lesser" Canada geese through the CRD on 25 October in three recent years.

Most of the taverneri seen in the autumn on the ECRD probably come from staging areas in upper Cook Inlet (Fig. 7). Quimby (1972) noted peak numbers of Canada geese at Chickaloon Flats in October of 1965 and 1970, and in other years large numbers have been seen there and in other parts of upper Cook Inlet just prior to major movements through Prince William Sound and the CRD area (J. Reynolds in litt., D. Timm pers. comm.). The breeding area of these birds is probably the Innoko River area, Kotzebue Basin, or possibly the inland fringes of the Yukon-Kuskokwim (Y-K) Delta. Many recoveries of birds banded in the former two areas have occurred in upper Cook Inlet and coastal Vancouver Island, indicating a coastal migration, whereas all recoveries of Y-K Delta geese, banded in the autumns of 1977 and 1978 at Cold Bay on the Alaska Peninsula, have been from the state of Washington or farther south, indicating a trans-Gulf migration (Table 4). Up to 73,500 taverneri have been censused in the Cold Bay area at one time in the autumn (Johnson et al. 1979). The phenology of migration of these Cold Bay birds is typically later than that of

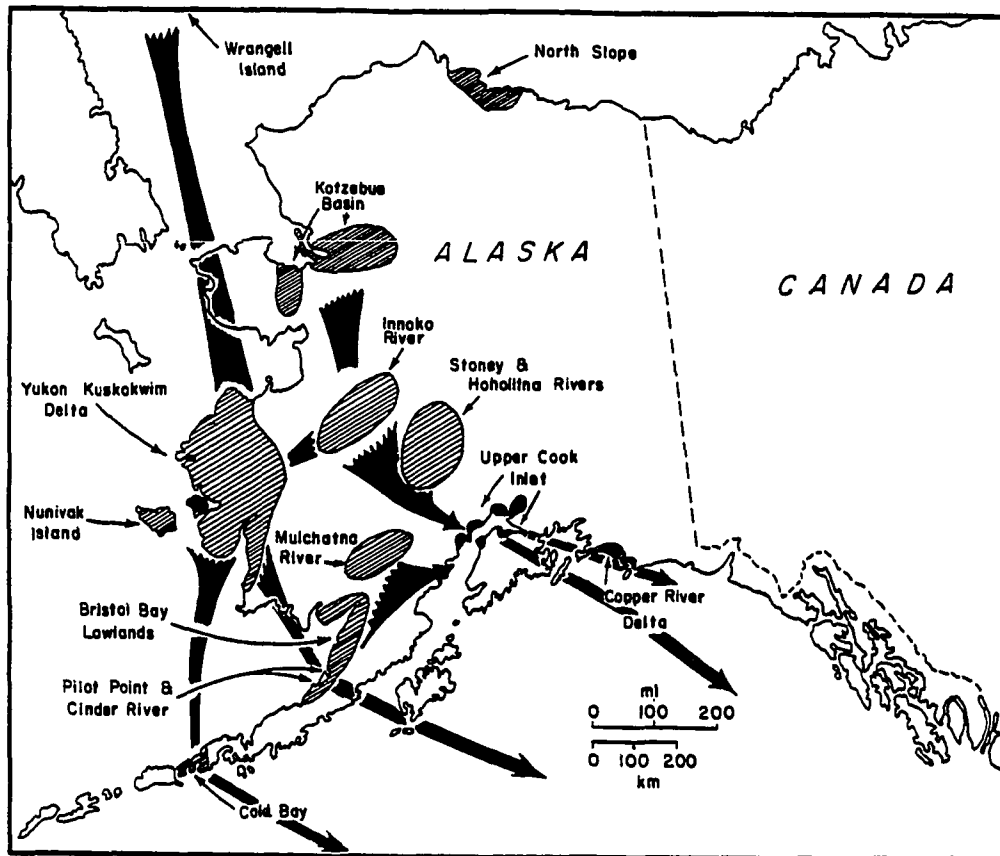


Figure 7. Alaska breeding, molting, and staging areas (streaked), and probable autumn migration routes of geese migrating through the Copper River Delta in spring or autumn.

Table 4. Recoveries of Taverner's Canada geese (B. c. taverneri) banded in Alaska.

| Reference | Banding Area | Years | Total banded | Total recoveries | ALASKA | | | | | | BRITISH COLUMBIA | | | |
|-----------|--------------------------|---------------|--------------|------------------|----------|-------------|----------------|----------------|----------------|----------|--------------------------------|----------|------------|--------|
| | | | | | Cold Bay | Y - K Delta | Nunivak Island | N Gulf Coast | Southeast | Interior | Coastal | Interior | WASHINGTON | OREGON |
| 1,4 | Y - K Delta | 1941,62-69,77 | 225 | 43 | 2 | | | | 1 ^a | | | 5 | 6 | 29 |
| 2,4 | Cold Bay | 1977,78,80 | 300 | 31 | 4 | 2 | 1 | | | | | 3 | 14 | 7 |
| 1 | Innoko River | 1949-54 | 806 | 102 | | | | 8 ^b | 1 | | 18 ^c | 41 | 32 | 2 |
| 1 | Kotzebue Basin | 1955-58,69 | 183 | 35 | | | | 4 ^b | | | 7 ^c | 14 | 10 | |
| 3 | North Slope ^e | 1971,75-78 | 1692 | 150 | | | | 2 | 1 | 6 | 1 ^c 16 ^d | 125 | | |
| 4 | Nunivak Island | 1979,80 | 120 | 10 | 3 | 2 | | | | | | | | 5 |

References: 1 Timm 1974
2 Timm and Sellers 1979, Timm 1980
3 King and Hodges 1980
4 Timm pers. comm.

Notes: a SW Prince William Sound
b upper Cook Inlet
c Vancouver Island
d including a few from Alberta
e including some parvipes

birds moving through Cook Inlet and the CRD. Departures from Cold Bay usually begin in the third week of October and peak in the last week of October or even the first week of November (D. Timm pers. comm.).

Although one of the Alaskan recoveries of taverneri banded on the Y-K Delta was in Prince William Sound, I feel that this is anomalous due to the lack of other coastal recoveries from this population. No banding has been done in the Kotzebue or Innoko areas since 1969 and 1954, respectively (Timm 1974), and none has been done on the inland fringes of the Y-K Delta. Some Canada geese banded on the North Slope of Alaska (Fig. 7) have been recovered in coastal Alaska and British Columbia, but these were all banded as non-breeding adults which may have been molt-migrants from anywhere in the state (King and Hodges 1979).

The first flocks of taverneri in both autumns seemed to lack juveniles. In 1978 I saw no juveniles prior to 8 October, but they were present after that time, being distinguishable by size and plumage among adults under good viewing conditions. In 1979 I saw no juveniles prior to early October, and could not distinguish age classes after that time owing to poor viewing conditions and the paucity of geese using the study area.

iii. Cackling Canada Goose (B. c. minima)

B. c. minima was the latest Canada goose migrant in the spring. Daily tallies of Canada goose subspecies indicated that the major

passage of this subspecies was from 5 to 15 May in 1978, and 5 to 14 May in 1979 (Figs. 3, 5). The 1979 migration is represented by a distinct late peak of dark geese in Fig. 3, although some of these were probably white-fronted geese. Flocks of minima showed less tendency than other Canada geese to fly inland of the barrier islands in 1979, and few stopped to rest or feed during either spring. Those that did stop usually stayed for several hours, and some as long as 24 hours, particularly towards the end of the migration period. R. Bromley (pers. comm.) also has observed frequent overnight stays by this subspecies on the WCRD. These lingering birds may have been subadults. Many minima may have regularly stopped in the spring prior to the earthquake. Shepherd (1965) reported finding "over 25,000 geese, mostly cackling geese, resting and feeding on the Bering River Flats," on 14 May 1965.

In spring, minima frequently passed in mixed flocks with white-fronts and Taverner's Canada geese. Flight altitudes were similar to those of taverneri, but flocks were larger (Table 3), and formations tended to be irregular. On 6 May, the peak of cackling goose migration in 1979, most flocks were over 100 and two were larger than 500 birds.

No minima were observed during autumn in this study, or prior to 23 October in 1980 (D. Herter pers. comm.), although they have apparently been present in "large numbers" during storm conditions in October of past years (Isleib and Kessel 1973, Isleib 1977). According to Nelson and Hansen (1959), arrival of autumn migrants at

the mouth of the Columbia River occurs in two waves, 15-20 October, and 25-30 October. The primary autumn staging areas for minima in Alaska are Pilot Point and the Cinder River, near the base of the Alaska Peninsula (Fig. 7). Heaviest use of this area is between 5 and 20 October, and during the last 5 years, large numbers have passed through or departed around 18-22 October (D. Timm pers. comm.). Clearly, minima is normally a trans-Gulf migrant in the autumn, as suggested by Nelson and Hanson (1959).

iv. Black Brant (Branta bernicla nigricans)

I saw few brant in the spring (Fig. 5) and none during autumn. Brant are well known as offshore migrants (Gabrielson and Lincoln 1959, Einarsen 1965, Isleib and Kessel 1973, Bellrose 1976). Arneson (1978, 1981) reported brant as being the only common goose seen migrating south of Cape St. Elias at the southern tip of Kayak Island (70 km S of the ECRD) in the spring of 1977 and 1978; Isleib and Kessel (1973) noted that this species passes through the offshore waters of the North Gulf Coast, and that in some years several thousand birds have passed along the coast during late May. Apparently, few pass inland of the barrier islands.

v. White-fronted Goose (Anser albifrons)

White-fronted geese appeared more frequently on the ECRD in

mixed than pure flocks during spring migration, most often with Taverner's Canada geese in April, and with cackling geese in May. Because they were the least common of the dark geese (with the exception of brant) passing in spring, and because of their frequent occurrence in mixed flocks, the daily checklists (Fig. 5) better reflect the timing of migration than do migration watch data. In both springs there appeared to be two waves of migration, one from 20-25 April, and the other coincident with the passage of cackling geese in May. These waves possibly represent birds (1) destined for different nesting areas, (2) of different age classes, or (3) of different subspecies. Most A. a. frontalis in the Pacific Flyway nest on or near the Y-K Delta (Miller and Dzubin 1968, Lensink 1969, King and Lensink 1971, Timm and Dau 1979), whereas most gambelli probably nest in Upper Cook Inlet (Timm and Sellers 1980).

White-fronted geese were the least likely to land of all geese passing in the spring, and I observed very few on the ground. A day's observations on Strawberry Reef on 7 May 1979 suggested that the majority were flying along the outer coast.

Patterns of autumn migration were similar in all three years of the study. Local hunters and fishermen commented on the scarcity of this species in 1979, the only year the fishermen could recall in which they did not see frequent flocks passing over the lagoon and barrier islands of the ECRD. In spite of intensive effort, especially in 1979 and 1980, I saw a total (including supplemental observations) of only about 2,400 in 1978, 1,400 in 1979, and 1,800 in 1980. The

only signs of any large-scale movements during the 3 years were: (1) a local fisherman's observation of approximately 50 flocks passing S along the west edge of the Ragged Mountains on 26 August 1978, and (2) a flock of 300 flying E on the evening of 31 August 1980. Few flocks stopped in the autumn for more than a few hours in any of the 3 years. Those which did linger tended to be small (<20 birds), usually composed of both adults and young, and normally stayed at most two or three days. An exceptional group may have lingered as long as a week in 1980.

These findings concur with those of Isleib and Kessel (1973) regarding the timing of the autumn migration, although in neither year did I observe a volume of passage comparable to any of the large concentrations of this species in past years; in fact, I saw no more than 150 on the ground at any one time, while the largest flying flock was the 300 birds seen on 31 August 1980. "A concentration estimated at 100,000 birds along the east bank of the Martin River.....on September 5, 1928" was reported by Gabrielson and Lincoln (1959:135), and according to Isleib and Kessel (1973:55), "the only concentration in recent years exceeding 30,000 birds is that [seen] by Solf of approximately 100,000.....on the flats of the Bering River between 1 and 4 September 1957..... This concentration built up during a period of easterly winds and departed en masse on 4 September when the winds shifted to the west". According to local residents, white-fronted geese commonly gathered by the thousands during late August in years prior to the earthquake.

It was enough, in fact, to prompt regular unofficial early opening of the goose hunting season on the ECRD during those years.

In autumn of 1979 and 1980 I took every opportunity to examine white-fronted geese closely to determine subspecies, and observed what I considered to be a number of gambelli, although most were frontalis. During late August and early September of 1979 and 1980, many of the small (1-15) groups and two larger ones (30, 31) appeared to be gambelli; most of these contained juveniles. The only concrete evidence of Tule geese from the CRD to date is from three individuals shot by hunters: one adult on 1 September 1971 on the WCRD (Bauer 1979:49), one adult on 2 September 1979 (head in Univ. of Alaska Museum, Fairbanks), and one neck-collared individual on 1 September 1980 on the WCRD (Timm and Sellers 1980).

There is evidence that non-breeders travel separately from family groups during the autumn migration: between 18 August and 1 September over the three years I saw a number of flocks ranging in size from 30 to 100 birds composed entirely of adults.

An unusual (according to local residents) late passage of white-fronted geese occurred from 10 to 13 October 1979, when I observed six flocks ranging in size from 11 to 70. With the exception of the 11, all of these were probably frontalis based on (1) their similar size to accompanying B. c. taverneri, and (2) measurements of two juveniles shot by hunters

The breeding and molting grounds of white-fronted geese observed in the autumn on the ECRD remain a mystery. Certainly some are

gambelli from Cook Inlet. The smaller subspecies, however, may come via Cook Inlet, across the Gulf of Alaska, or down the Copper River Valley. Flocks that appear moving east along the barrier islands are probably coming from Cook Inlet via Prince William Sound, while others that appear flying down the west side of the Ragged Mountains may have come down the Copper River. Isleib and Kessel (1973) felt that autumn migrants come via Prince William Sound or across the Gulf of Alaska, while Lensink (pers. comm.), and Shepherd (pers. comm.) feel that some probably come down the Copper River. I believe that evidence points most consistently to the Cook Inlet route. Concentrations of up to 10,000 have been observed in upper Cook Inlet marshes in late August and early September (Timm pers. comm.). There is evidence that some white-fronted geese of the Pacific Flyway come from breeding and molting areas other than the Yukon-Kuskokwim Delta, where King and Lensink (1971) felt the entire population originated. In addition to as many as 5,000 gambelli (M. Wege in litt.) which probably all nest and molt in Cook Inlet, there are small numbers of (presumably) frontalis known to be nesting in the Bristol Bay Lowlands, and along the Stony, Hoholitna, and Mulchatna River drainages (Fig. 7) (Gabrielson and Lincoln 1959:134, Timm and Sellers 1980). Sandhill cranes passing through the ECRD in autumn and spring migration to and from wintering grounds in California are also believed to nest on the Alaska Peninsula and/or Bristol Bay Lowlands (Herter 1982).

About 10% of the recoveries of frontalis banded in the Innoko

River Valley have been in the Pacific Flyway, although these were all banded as non-breeding adults which may have been molt-migrants from the Y-K Delta. All recoveries of young of the year banded in the Innoko area have been from the Central Flyway (Lensink 1969).

The regular timing of the autumn migration on the ECRD and the small year to year fluctuations in numbers indicate that a particular population of frontalis traditionally uses this route. The migration of Pacific Flyway white-fronted geese appears to be trimodal, with three "waves" of arriving birds at the Klamath Basin in northern California: (1) late August, (2) mid to late September, and (3) about 1 November (E. J. O'Neill in litt.). The migration through the CRD consistently corresponds to the first of these waves; very few white-fronted geese are seen after mid-September. Since few autumn migrants use staging areas between south-coastal Alaska and the Klamath Basin, and some researchers (e.g. Bellrose 1976) believe that essentially non-stop flights are involved, it is likely that migrants through the CRD are part of the first wave of arrivals in California. Although most autumn migrants through the CRD are probably not from the Y-K Delta, to explain the occasional massive concentrations of frontalis observed on the ECRD and Bering River Delta prior to the earthquake of 1964, one would have to involve the Y-K Delta birds, since they comprise 95% of the Pacific Flyway contingent (Timm and Dau 1979). If Y-K Delta birds were involved in these concentrations, the question arises as to why these buildups only occurred in August and early September, rather than during the second and third waves of

migration, when weather tends to be much worse in the Gulf of Alaska. The answer may lie in differences in prevailing wind patterns in the Gulf during August as compared to October. In August winds south of the Alaska Peninsula tend to blow from the WSW, whereas during September and October they are from the NW or WNW, and are more favorable for trans-Gulf migration (Brower et al. 1977) (see Discussion).

White-fronted geese passed at a variety of altitudes in the autumn. Some of the largest flocks were observed at the greatest heights (300-900 m).

vi. Lesser Snow Goose (Chen caerulescens caerulescens)

Snow goose migration was also bimodal in both springs of the study (Fig. 3), as well as in 1980 (23 April and 1 May; D. Herter pers. comm.). Snow geese often occurred in mixed flocks with taverneri, but in general tended to be at higher altitudes, occasionally over 1,200 m. This species regularly gathers on the Kenai River Delta in upper Cook Inlet in the spring, where numbers peaked at about 15,000 on 21 and 22 April 1979. Normally the first flocks arrive there on 10-12 April, numbers peak during 17-23 April, and last departures are 3-5 May (D. Timm pers. comm.).

Snow geese were relatively unpredictable migrants in autumn, and appeared later and in greater numbers in 1978 than in 1979. Since they probably came along the same migration routes as taverneri, the

same factors were likely responsible for the decline in visible migration of both from 1978 to 1979. With the possible exception of several early family groups in late September of 1979, none stayed longer than 24 hours on the ECRD in either year. None were seen flying at altitudes greater than 300 m.

III. HABITAT RELATIONSHIPS

A. Habitat Use

i. Spring

Spring migration of geese on the ECRD occurred over a relatively short period of time, during which a large number of birds passed. With the exception of B. c. occidentalis and B. c. minima, very few geese stopped to rest or feed on the ECRD. Most of those which stopped in 1979 did so for much less than 12 h. B. c. occidentalis used both the Freshwater Meadow and Saltmarsh; they particularly favored standing water and muddy substrates, both of which offered easy grubbing for roots and new shoots of vegetation. B. c. taverneri used similar habitats, most frequently in the Saltmarsh. B. c. minima and C. caerulescens used only the Saltmarsh in 1979, although I saw 30 cackling geese land and feed briefly at the edge of some standing water in the Freshwater Meadow in 1978. A. albifrons used only the Saltmarsh in 1979.

On the WCRD, R. Bromley (pers. comm.) has observed taverneri, A. albifrons, and C. caerulescens using "wet sedge meadows", which are probably analagous to some of the sedge-dominated areas of the Freshwater Meadow on the ECRD except that they have fewer shrubs.

ii. Autumn

The Freshwater Meadow ground transect proved to be imprecise in reflecting short-term changes in habitat use because of the small area sampled and large variations in flock size, but adequately demonstrated seasonal changes. B. c. occidentalis made more intensive use of the ECRD than any other geese in both autumns, and used both Freshwater Meadow and Saltmarsh heavily (Fig. 8). These geese almost exclusively used the Saltmarsh until a period of transition during the last 10 days of August and first week of September. The Saltmarsh of Strawberry Reef was particularly heavily used during August by occidentalis; S. Murphy (pers. comm.) found over 1,000 there on 15 August 1978. During the period of transition flocks did progressively more feeding in the Freshwater Meadow during the day, but continued to roost at night in the Saltmarsh, particularly at the mouths of sloughs. By about 5 September, virtually all feeding activity was in the Freshwater Meadow, while the Saltmarsh continued to serve as a roosting area and as a refuge when the birds were harassed by bald eagles (Haliaeetus leucocephalus) or hunters. Some birds also roosted in large ponds on the northern edge of the Freshwater Meadow and

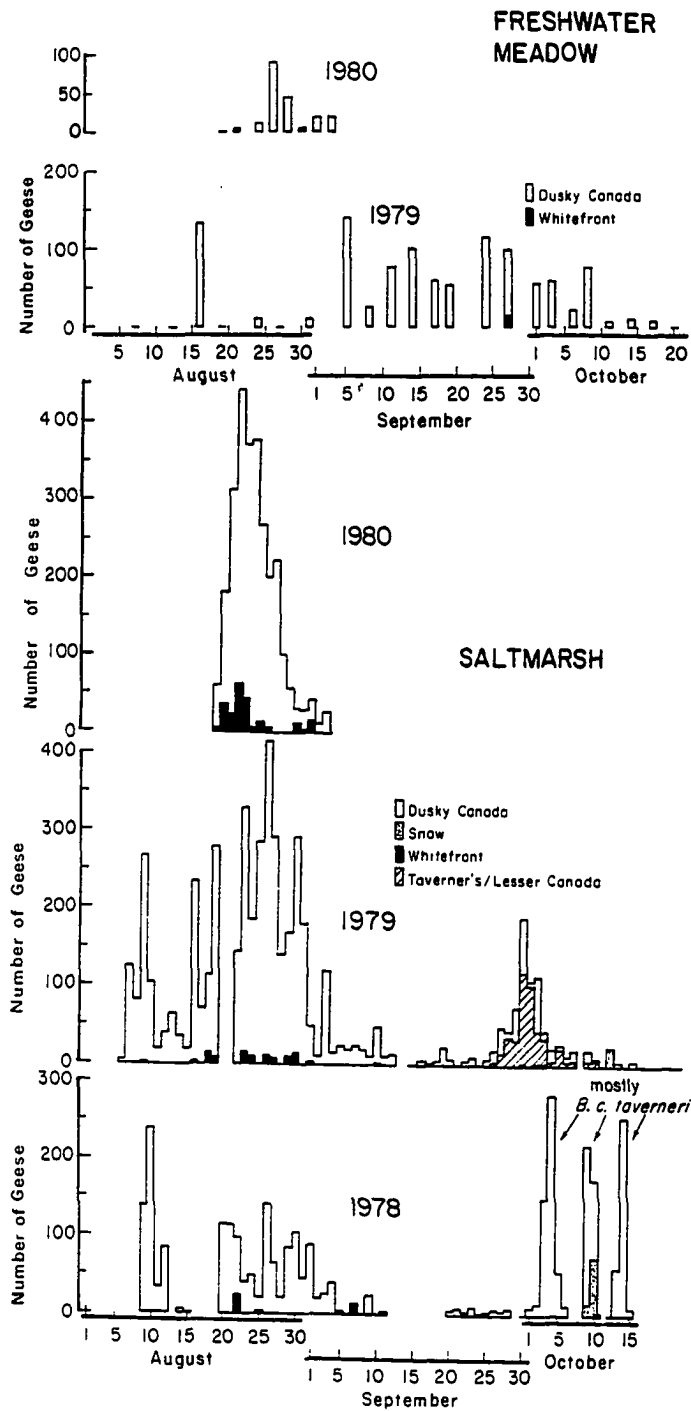


Figure 8. Patterns of autumn habitat use by geese on the eastern Copper River Delta, Alaska. Ordinate is mean number of geese counted daily on a delineated census area (Saltmarsh), and number of geese within effective width of a variable-width belt transect (Freshwater Meadow). Gaps indicate missing data.

possibly in the Shrub Marsh.

Virtually the entire Saltmarsh and Freshwater Marsh were used for feeding during August and September, respectively. During late September and early October flocks of occidentalis in the Freshwater Meadow were increasingly associated with areas of shallow standing water which had poorly defined shorelines and extensive emergent vegetation.

Judging from the numbers of geese I observed while walking the Freshwater Meadow line transect (Fig. 2) and from the observation tower during migration watches in September and October, there was little change in the population of occidentalis on the ECRD from mid-August until late September in either 1978 or 1979.

With the exception of one or two flocks in the autumn of 1978, B. c. taverneri used only the Saltmarsh for resting and feeding during autumn migration. They were particularly abundant during the storm of 7-9 October 1978, and under similar conditions on 8-10 October 1980 (D. Curran and D. Herter pers. comm.). At times when migration was heavy, they were abundant but very transient (as in spring 1979) on the Saltmarsh of Strawberry Reef. Very few flew over or made use of the Saltmarsh of the mainland ECRD on these days of intensive migration, especially when winds were offshore, as they were in 1979.

Snow geese used only the Saltmarsh and intertidal mud and sandflats. Some flocks spent their entire brief stay loafing on the mudflats.

White-fronted geese used the Saltmarsh, and, rarely, the Freshwater Meadow. In the latter habitat they were always in emergent vegetation in or at the edge of ponds such as those frequented by occidentalis.

B. Successional Changes Resulting from the Earthquake

i. Pre-Earthquake Condition

Drainage and vegetation patterns in pre-earthquake photographs indicate that the entire Freshwater Meadow (Fig. 2) was formerly under at least occasional tidal influence, and therefore was Saltmarsh. The uplift raised this entire Saltmarsh and varying extents of lower-lying unvegetated mudflats above even the highest spring tides. The area of these former mudflats on the ECRD is greatest between Russian River Slough and Mirror Slough. The amount of uplift beyond that necessary to raise the entire vegetated area above tidal influence has not been determined on the ECRD, but appears to have been at least 0.5 m. Plafker (1969) inferred approximately 3.05 m (10 ft) of uplift for the Bering River-Controller Bay area versus only 2.4 m (8 ft) for the WCRD. Extensive areas of mudflats were also raised above tidal influence on the Bering River Delta, as Plafker's findings suggest (Hagen and Meyer 1978).

Dense vegetation was restricted to natural levees throughout

most of the pre-earthquake Saltmarsh of the ECRD. The remainder of the Saltmarsh had either scattered patches of vegetation or was bare ground, possibly with sparse growths of Puccinellia spp., Eleocharis sp., or Triglochin palustris, which would not show up well on aerial photographs. Vegetative cover was complete only in the few areas where permanent ponds were and still are numerous. Overall, dense vegetation covered less than 50% of the land area. This situation was in direct contrast to the pre-earthquake WCRD, which had essentially complete vegetative cover, and abundant permanent ponds.

ii. Present Condition

The present (1980) conditions of both the ECRD and WCRD reflect differences in their pre-earthquake vegetation. The WCRD is still characterized by many permanent ponds, well-developed sedge basins, and shrub invasion which is largely limited to levees. On the ECRD there are few permanent ponds, more diverse and interspersed vegetation communities, and more widespread shrub invasion. Large moss-dominated areas are unique to the ECRD as well; their distribution suggests that mosses rapidly colonized almost all of the mesic and well-drained bare ground portions of the uplifted Saltmarsh and mudflats after the earthquake. Now, shrubs have taken over the well-drained habitats, but mosses still predominate in the more mesic areas. Some plant species common on the WCRD are extremely rare or absent in the Freshwater Meadow of the ECRD, for example Hedysarum

alpinum, Dodecatheon Jeffreyi, Plantago macrocarpa, and Lathyrus palustris.

Because of the above evidence, and the reputation of the ECRD as a staging area for snow geese and white-fronted geese prior to the earthquake, I suggest that the pre-earthquake vegetation was similar in species composition to that found in upper Cook Inlet saltmarshes which are presently used as staging areas by geese. There Triglochin maritimum, T. palustris, Plantago maritima, and Puccinellia spp. are abundant and known to be preferred goose foods in these saltmarshes (see Food Habits), and these were probably the species which attracted autumn migrants to the ECRD. R. Baxter (pers. comm.) a biologist who hunted on the ECRD prior to the earthquake, recalled that "goosetongue" (Plantago maritima) was one of the common plants in the Martin River Slough area, and also that there were small amounts of eelgrass (Zostera marina) in the lagoon. Both species of Triglochin are still fairly common in the Freshwater Meadow, especially within a few km east of Cottonwood Dunes, but neither species is particularly vigorous or abundant, and both are probably declining.

C. Successional Trends

i. Freshwater Meadow

Plant succession has been occurring rapidly in the Freshwater

Meadow since the 1964 uplift, and substantial changes are evident even since the area was mapped by Scheierl and Meyer (1977) in 1976. The most dramatic changes are in the shrub component, and the rate of these changes appears to be increasing. Shrubs were inconspicuous in the Freshwater Meadow as recently as 1974, even though the first few seedlings were probably growing within a year or two of the earthquake, as was observed on the WCRD (Crow 1971). Now thick bands of shrubs, primarily alder, are found on the better-drained sites, especially natural levees, and scattered shrubs are found virtually throughout the Freshwater Meadow. Although aerial photographs at the present time (1980) would probably indicate that dense thickets cover only a few percent of the Freshwater Meadow, shrubs already seriously impair visibility.

Trends in abundance of other plants are not so obvious, but as mentioned previously, it is reasonable to assume that halophytes dramatically declined as presently dominant species invaded. There were still numerous patches (pans) of bare ground in 1974, especially in the Martin River and Cudahy Slough areas, but almost all of these are now colonized at least sparsely, primarily by Carex lyngbyaei.

ii. Saltmarsh

Vegetation has been slower to develop in the area now influenced by tides, and has been much more difficult to trace since sparse growths of typical Saltmarsh plants can be almost invisible on aerial

photography. Nevertheless, it appears that much of the present vegetation (Fig. 2) has developed from bare ground since 1974. The Puccinellia zone is extending seaward, and the density of plants in the already colonized areas is increasing.

The rates at which this expansion of the Saltmarsh will occur, and its ultimate limits, largely depend on siltation rates and the propagation capabilities of the pioneering species, especially Puccinellia spp. Siltation rates may be considerable at present, judging from measurements made recently at Susitna Flats in Cook Inlet; several centimeters accumulated in one year in the outermost plant community of that saltmarsh (Vince 1981).

IV. FOOD HABITS

A. Autumn

i. Dusky Canada Goose

a. General Features of the Diet

At least 26 species of plants representing 13 families were found in dusky Canada goose stomachs (Table 5). There was tremendous variability among individuals, much of which was probably attributable to microhabitat differences among areas in which they were feeding prior to being shot. Fifteen species of monocots of four

Table 5. Food items found in proventriculi of dusky Canada geese (*Branta canadensis occidentalis*) on the eastern Copper River Delta, Alaska during fall of 1978 and 1979. Numbers of plant species in each family are given in parentheses following family names.

| FOOD ITEM | 8-31 AUG N=10 | | 1-15 SEPT N=36 | | 16-30 SEPT N=27 | | 1-15 OCT N=14 | | ENTIRE AUTUMN (ave. of 4 periods) | |
|--|------------------|-----------------|-------------------|------|--------------------|------|------------------|------|--------------------------------------|------|
| | %F ^a | %V ^b | %F | %V | %F | %V | %F | %V | %F | %V |
| MOSS | | | 5.6 | 1.1 | 7.4 | tr | 7.1 | tr | 5.0 | 0.3 |
| EQUISETACEAE (1) | | | | | | | | | | |
| <i>Equisetum arvense</i> | 20 | 18.5 | 27 | 3.8 | 29.6 | 22.1 | 35.7 | 28.6 | 28.1 | 18.2 |
| JUNCAGINACEAE (2) | * | | 44.4 | 30.0 | 37.0 | 22.9 | *? | | 20.4 | 13.2 |
| <i>Triglochin maritimum</i> | * | | 5.6 | 3.2 | 11.1 | 3.4 | | | 4.2 | 1.6 |
| <i>Triglochin palustris</i> | * | | 41.7 | 26.8 | 33.3 | 19.5 | *? | | 18.8 | 11.6 |
| GRAMINEAE (7) | 40 | 13 | 44.4 | 30.2 | 37.0 | 21.5 | 21.4 | 14.3 | 35.7 | 19.8 |
| <i>Agrostis</i> spp. ^c | * | | 25.0 | 16.9 | 18.5 | 11.3 | | | 10.9 | 7.6 |
| <i>Calamagrostis</i> spp. ^d | * | | 5.6 | 0.9 | 3.7 | 1.9 | | | 2.3 | 0.7 |
| <i>Deschampsia caespitosa</i> | 10 | tr | 8.3 | 3.4 | * | | 7.1 | 0.1 | 6.4 | 0.9 |
| <i>Poa eminens</i> | | | 8.3 | 4.2 | 7.4 | 0.3 | 14.3 | 14.2 | 7.5 | 4.7 |
| <i>Puccinellia nutkaensis</i> | 40 | 13 | 8.3 | 2.8 | 14.8 | 8.0 | | | 15.8 | 5.9 |
| CYPERACEAE (5+) | 50 | 41 | 33.3 | 12.2 | 29.6 | 21.9 | 28.5 | 7.4 | 35.4 | 20.6 |
| <i>Eriophorum</i> spp. ^e | | | 5.6 | 0.6 | * | | | | 1.4 | 0.2 |
| <i>Eleocharis</i> spp. ^f | * | | 8.3 | 5.0 | 14.8 | 14.8 | 7.1 | 7.1 | 7.6 | 6.7 |
| <i>Carex lyngbyaei</i> | 50 | 26 | 11.1 | 4.2 | 3.7 | 3.7 | 14.3 | 0.2 | 19.8 | 8.5 |
| <i>Carex ramenskii</i> | 20 | 15 | 8.3 | 2.4 | | | | | 7.1 | 4.4 |
| <i>Carex mackenziei</i> | * | | | | | | | | | |
| <i>Carex</i> sp. | | | | | 11.1 | 3.4 | 14.3 | 0.1 | 6.4 | 0.8 |
| JUNCACEAE (1+) | * | | 25.0 | 7.7 | 7.4 | 7.3 | 21.4 | 21.4 | 13.5 | 9.1 |
| <i>Juncus alpinus</i> | * | | 25.0 | 7.7 | 3.7 | 3.6 | 21.4 | 21.4 | 13.5 | 8.2 |
| <i>Juncus</i> sp. | | | | | 3.7 | 3.7 | | | 0.9 | 0.9 |
| SALICACEAE (1) | | | 2.8 | tr | | | | | 0.7 | tr |
| <i>Salix</i> sp. | | | | | | | | | | |
| BETULACEAE (1) | | | 5.6 | 2.4 | 3.7 | 3.2 | 7.1 | 7.1 | 4.1 | 3.2 |
| <i>Alnus sinuata</i> | | | | | | | | | | |
| CARYOPHYLLACEAE (1) | | | 5.6 | 4.6 | | | | | 1.4 | 0.8 |
| <i>Stellaria</i> sp. | | | | | | | | | | |
| RANUNCULACEAE (1) | 20 | tr | | | | | | | 5.0 | tr |
| <i>Ranunculus cymbalaria</i> | | | | | | | | | | |
| ROSACEAE (1+) | | | 2.8 | 0.1 | | | 7.1 | tr | 2.5 | tr |
| <i>Potentilla</i> sp. | | | | | | | | | | |
| LEGUMINOSAE (1) | | | | | 3.7 | 0.2 | | | 0.9 | tr |
| <i>Lathyrus palustris</i> | | | | | | | | | | |
| PLANTAGINACEAE (1) | 40 | 27 | 5.6 | 3.8 | | | | | 11.8 | 7.7 |
| <i>Plantago maritima</i> | | | | | | | | | | |
| INSECTA | | | 5.6 | 2.2 | | | | | 0.7 | tr |
| Tipulidae (adult) | | | | | | | | | | |
| unidentified: root | | | 11.1 | 1.6 | 7.4 | tr | 21.4 | 16.4 | 10.0 | 4.5 |
| leaf | | | 5.6 | 0.3 | | | 14.3 | 4.6 | 5.0 | 1.2 |
| seed | | | 2.8 | tr | 3.6 | tr | | | 1.6 | tr |
| TOTALS | | | 99.5 | 100 | 99.1 | 99.8 | | | 98.8 | |

* eaten by geese according to other observations, but not found in collected birds

^a percent frequency of occurrence; ^b mean percent volume (see Methods)

^c largely *A. alaskana*, but also probably some *A. exarata* and *A. geminata*

^d largely *C. deschampsiodes*, but also some *C. inexpansa*

^e *E. russeolum* or *E. scheuchzeri*

^f *E. palustris* or *E. kamschatica*

families (Cyperaceae, Gramineae, Juncaginaceae, and Juncaceae) made up 69% of the total volume of the diet over the course of the autumn, and together with Equisetum arvense, contributed 87% of the total. Dicots were thus relatively unimportant, and most were probably ingested incidentally (e.g. Salix sp., Ranunculus cymbalaria, Potentilla sp.), as were mosses. Results of the only other quantitative study of autumn food habits of geese in northern coastal North America (Prevett et al. 1979) were remarkably similar; that study found over 40 species in the diet of lesser snow geese over a much larger geographic area, but Cyperaceae, Juncaginaceae, Equisetaceae, and Gramineae were still the most important families.

Leaves were the most important food by volume, contributing more than seeds and roots combined (Table 6). Overall, both methods of interpreting the data (mean percent frequency of occurrence and mean percent volume) ranked the same food items as most important (Spearman rank correlation $r = 0.88$, $P < 0.001$; Fig. 9).

b. Changes Through the Autumn

There were marked changes in the proportions of different taxa in the diet of dusky Canada geese as the autumn progressed (Table 5, Figs 10, 11), attributable to one or more of the following factors: (1) changes in habitat use and thus plant availability, (2) changes in preferences for and thus selection of parts of particular plants, and (3) changes in abundance of food due to depletion by the geese. A

Table 6. Parts of plants found in proventriculi of dusky Canada geese on the eastern Copper River Delta, Alaska during fall of 1978 and 1979. Numbers are mean % volumes (see Methods).

| FAMILY | PART | 8-31 AUG | 1-15 SEPT | 16-30 SEPT | 1-15 OCT | ENTIRE AUTUMN | |
|--------------------|----------------------|-------------------------|------------|------------|------------|---------------------------|-----|
| | | N=10 %V ^α | N=36 %V | N=27 %V | N=14 %V | (ave. of 4 periods) %V | |
| EQUISETACEAE | leaf | 18.5 | 2.4 | 19.9 | 29.6 | 17.5 | |
| | root | | 1.4 | 2.2 | | 0.9 | |
| | seed | | | | | | |
| JUNCAGINACEAE | Triglochin maritimum | leaf | * | 3.2 | 3.4 | 1.7 | |
| | | root | | | | | |
| | | seed | tr | | | | tr |
| | Triglochin palustris | leaf | * | 12.2 | 8.4 | | 5.2 |
| | | root | * | 14.6 | 11.1 | | 6.4 |
| | | seed | | | | | |
| GRAMINEAE | leaf | 8.5 | 2.8 | 7.8 | | 4.8 | |
| | root | | | | | | |
| | seed | 4.5 | 27.4 | 13.4 | 14.3 | 14.8 | |
| CYPERACEAE | leaf | 41.0 | 11.8 | 7.1 | 7.1 | 16.8 | |
| | root | * | 0.4 | 14.8 | 0.4 | 3.9 | |
| | seed | | | | | | |
| JUNCACEAE | leaf | | | 1.5 | 3.6 | 1.3 | |
| | root | | | 2.2 | 17.9 | 5.0 | |
| | seed | * | 7.7 | 3.6 | | 2.8 | |
| BETULACEAE | leaf | | | | | | |
| | (cone) root seed | | 2.4 | 3.2 | 7.1 | 3.2 | |
| PLANTAGINACEAE | leaf | 27.0 | 3.8 | | | 7.7 | |
| | root | | | | | | |
| | seed | | | | | | |
| OTHER (5 families) | leaf | 0.5 | 4.7 | 0.2 | | 1.4 | |
| | root | | | | | | |
| | seed | | | | | | |
| UNIDENTIFIED | leaf | | 0.3 | | 4.6 | 1.2 | |
| | root | | 1.6 | | 16.4 | 4.5 | |
| | seed | | | | | | |
| TOTALS | LEAF | 95.5 | 41.1 | 48.3 | 36.8 | 55.4 | |
| | ROOT | 0 | 19.1 | 30.4 | 41.1 | 22.7 | |
| | SEED | 4.5 | 37.4 | 20.2 | 21.7 | 21.0 | |
| | | 100. | 97.6 | 98.9 | 99.9 | 99.1 | |

^α see Methods

* eaten by geese according to other observations, but not found in collected birds

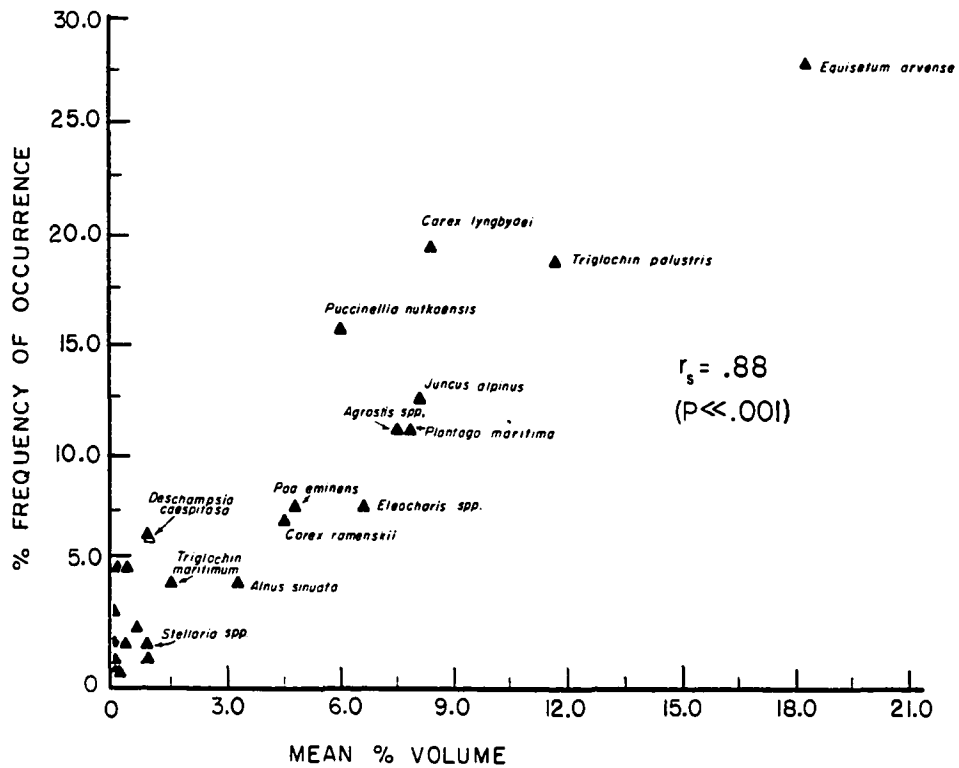


Figure 9. Relationship between % frequency of occurrence and mean % volume (=aggregate % volume) of food plants found in stomachs of dusky Canada geese collected on the eastern Copper River Delta in autumn 1978 and 1979. Each point is the average of four separate time periods (see Table 5).

change from predominantly salt-tolerant species to a wide variety of foods occurred concurrent with the shift of feeding activities from Saltmarsh to Freshwater Meadow (see Habitat Use). The proportion of leaves in the diet was very high in August, but rapidly declined as use of seeds and, later, roots increased (Table 6).

Geese ate only one particular part of some species, but in the case of other species they shifted emphasis from one part to another as the season progressed. Most plants from which leaves were essentially the only parts eaten (Plantago maritima, C. ramenskii, C. lyngbyaei) disappeared from the diet over time. Equisetum arvense was an exception in that leaves, stems, and shoots were virtually the only parts eaten, yet it increased in importance as the former three species declined, and constituted most of the leaf material in the diet in October (Table 6). Geese ate only the inflorescences of grasses (with the exception of Puccinellia nutkaensis), but switched from leaves or seeds to roots of some other taxa (e.g. Triglochin palustris, Eleocharis spp., Juncus alpinus). The change in feeding habitat affected the part of T. palustris which was eaten. In August, the leaves of virtually all plants of this species were grazed in the Saltmarsh, but the roots were seldom pulled up. In the Freshwater Meadow, where the substrate was soft and mossy and the plants larger, bulbs were the primary target. Often geese clipped and discarded attached leaves before ingesting the bulbs. Sandhill cranes feeding on the ECRD in autumn are even more careful in their handling of this food; they remove any leaves and the sheath of the bulb before

ingesting it (Herter 1982).

c. Food Availability vs. Use

Geese positively selected some taxa, ate others roughly in proportion to their abundance, and avoided others (Figs. 10, 11). The most consistent positive selection was for Equisetum arvense, Carex lyngbyaei, Puccinellia nutkaensis, and Plantago maritima in the Saltmarsh, and for T. palustris, Equisetum arvense, Agrostis spp., and Juncus alpinus in the Freshwater Meadow. Moss was only eaten incidentally (probably with T. palustris), although it was by far the most abundant plant in the area. No previous studies (e.g. Markgren 1963, Prevett et al. 1979) have found more than small, probably incidental ingestion of moss, confirming that it is a very poor food for geese. Most Saltmarsh plants were neutrally or positively selected; a notable exception was Potentilla egedii, which was ubiquitous in both habitats, but never eaten.

According to observations of the vegetation and feeding geese, the most preferred foods in the Saltmarsh were T. palustris and T. maritimum, both of which were uncommon and patchy in distribution. Since there were only 24 vegetation plots and 10 geese collected from the Saltmarsh in August, it is not surprising that (1) T. maritimum did not occur in the plots, and (2) both species were absent from the stomachs of collected birds. In addition, seeds of Deschampsia caespitosa were frequently consumed in the Saltmarsh in late August,

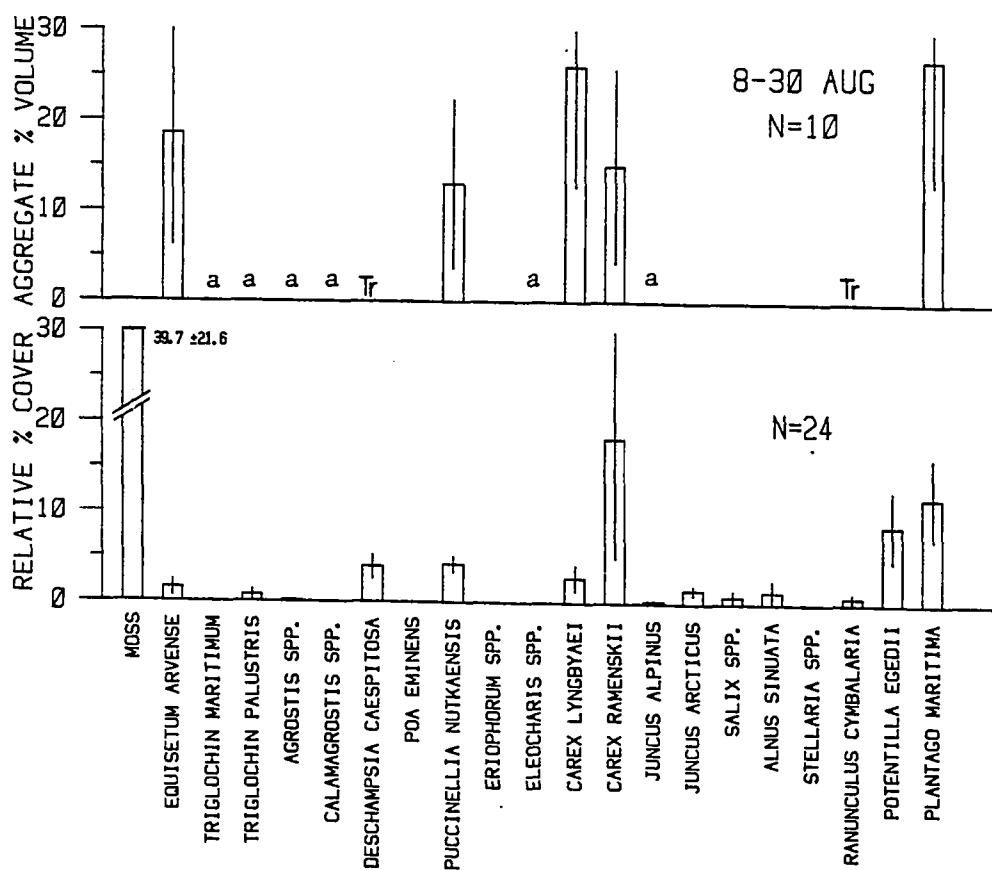


Figure 10. Availability of Saltmarsh food plants on the eastern Copper River Delta, Alaska (bottom), and their use by dusky Canada geese during August of 1978 and 1979. Values are means \pm SE. Notes: a - not found in collected birds but eaten according to other observations. Tr - trace.

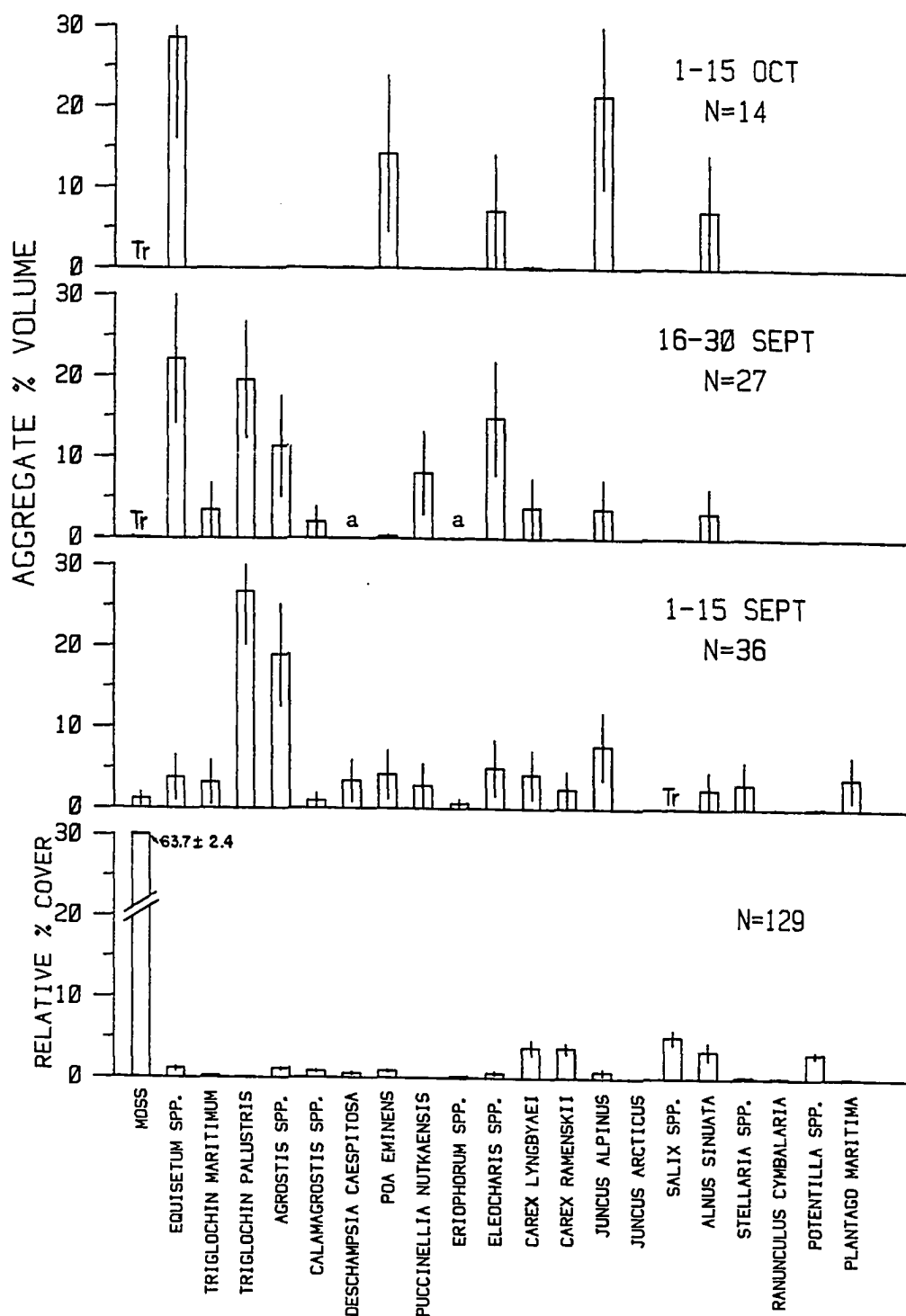


Figure 11. Availability of Freshwater Meadow food plants on the eastern Copper River Delta (bottom), and their use by dusky Canada geese during September and October of 1978 and 1979. Values are means \pm SE. Notes: a - not found in collected birds but eaten according to other observations. Tr - trace.

and were under-represented in the collected birds.

Geese avoided some convenient and presumably nutritious parts of extremely common plants. The seeds of Carex lyngbyaei and C. ramenskii were never eaten by dusky Canada geese, although a few were found in B. c. taverneri stomachs (see below); neither were the seeds of Plantago maritima or the leaves of most grass species eaten, even during the period when leaves of other taxa (C. lyngbyaei, C. ramenskii, Plantago maritima, Triglochin spp.) were a major component of the diet. Owen and Kerbes (1971) noted that abundant Plantago maritima seeds were also avoided by barnacle geese (Branta leucopsis) in the autumn. The avoidance of these potential foods may be due to plant defense compounds which are toxic or unpleasant to geese. Plant toxins have been shown to play important roles in foraging by other vertebrate herbivores (e.g. Bryant and Kuropat 1980).

ii. Other Geese

Geese other than dusky Canada geese made relatively little use of the ECRD in the autumn, and consequently I have little information on their diets. Of four B. c. taverneri collected in October which contained food, two contained mostly Equisetum arvense shoots, the third Puccinellia nutkaensis leaves, and the fourth unidentified root material. Two of these had also eaten Carex lyngbyaei seeds, a surprise because no dusky Canada geese ate this abundant food. From observations of feeding birds, it appeared that the major foods of

Taverner's Canada geese were Equisetum arvense (particularly in the area between Russian River Slough and Cottonwood Slough), entire small seedlings or ramets of Juncus alpinus and Eriophorum spp. (near the interface of the Saltmarsh and Freshwater Meadow), and Puccinellia nutkaensis.

White-fronted geese appeared to feed almost exclusively on leaves of Carex ramenskii, C. lyngbyaei, T. palustris, and Puccinellia nutkaensis in the Saltmarsh, and probably Eleocharis spp. and C. lyngbyaei leaves, and T. palustris bulbs in the Freshwater Meadow.

B. Spring

From observations of feeding birds and examination of vegetation, the main foods of dusky Canada geese on the ECRD in the spring appeared to be the new shoots of Carex lyngbyaei and C. ramenskii; the upper portions of these were discarded if the shoot exceeded about 5 cm in length. The spring phase of Equisetum arvense was also important, as well as new leaves of Puccinellia nutkaensis and Plantago maritima. Some root material and seedlings or ramets of Juncus alpinus were also eaten.

Taverner's Canada geese fed primarily on Puccinellia nutkaensis leaves and shoots of C. ramenskii. B. c. minima probably fed on a wide variety of new green shoots which were available by early May. Plantago maritima leaves appeared to be their major food in the

Little River Slough area.

V. THE INFLUENCE OF WEATHER ON MIGRATION

A. Synoptic Weather Systems

I interpreted the apparent effects of synoptic weather systems on visible migration with caution for several reasons. Resolution was necessarily sacrificed in transferring information from daily weather maps to the generalized weather maps, with the loss of some subtleties which would be helpful in interpreting each day's observations. In addition, birds probably respond rapidly to changes in weather -- changes which may be totally obscured if one examines successive weather maps, without considering the likely sequence of intervening events.

Spring migration was heaviest when the CRD was under the influence of high pressure systems to the S, as it was during April 1979 (Fig. 12). During early autumn, there was no clear relationship between migration and synoptic weather, although the heaviest migration occurred when high pressure centers were close to the ECRD (Fig. 13). Later in the autumn, when low pressure centers became more frequent and more intense, migration was most pronounced as strong lows weakened and moved onshore west of the CRD (e.g. 3, 10, 11, 13 Oct. 1978; 13 Oct. 1979). Weakening lows moving to the S of the CRD (e.g. 11, 12, 17, 18 Oct. 1979) had less predictable effects (Fig.

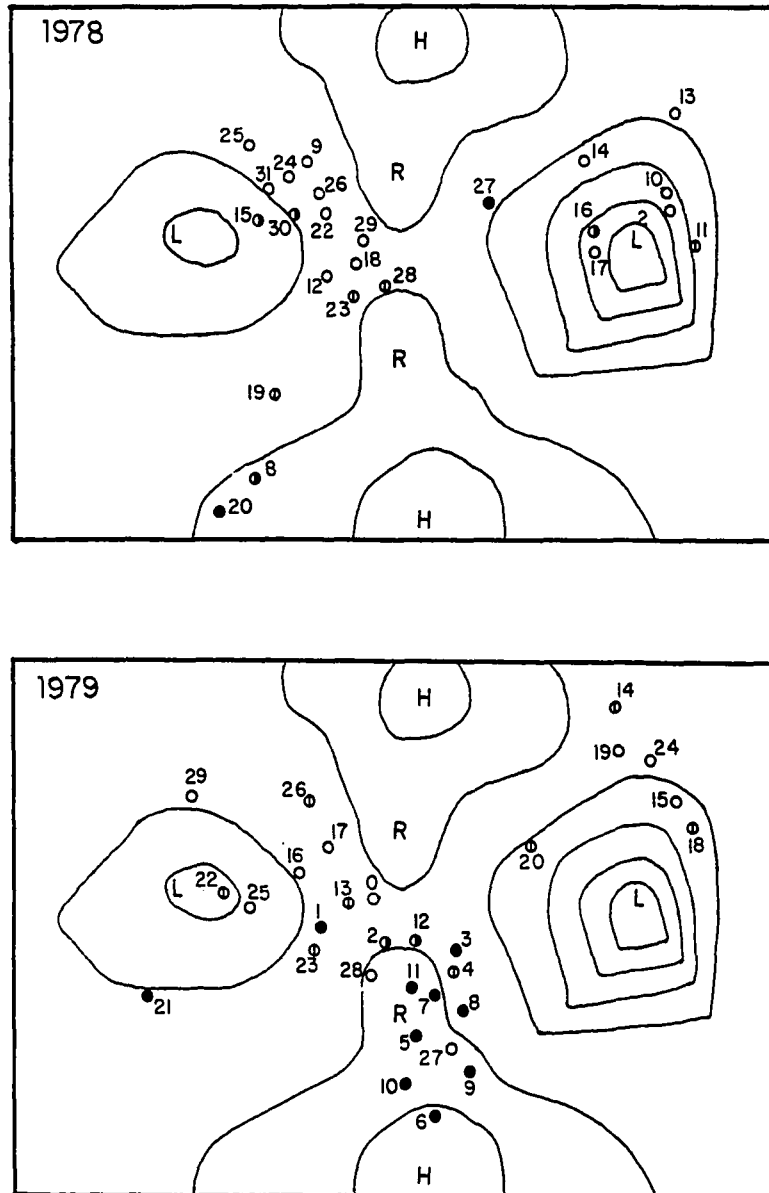


Figure 12. Location of the Copper River Delta, Alaska, on successive days during spring 1978 and 1979 relative to generalized synoptic surface weather features (map from Blokpoel and Gauthier 1980). High (H) and low (L) pressure systems are depicted as well as ridges (R) of high pressure. A weak low is on the left and a strong low on the right. Numbers correspond to dates (1=16 April, 16=1 May, 31=15 May). Estimated daily migration volume is indicated by the type of circle: O 0-1,200 geese; ⊕ 1,200-2,400; ⊙ 2,400-4,800; ● >4,800.

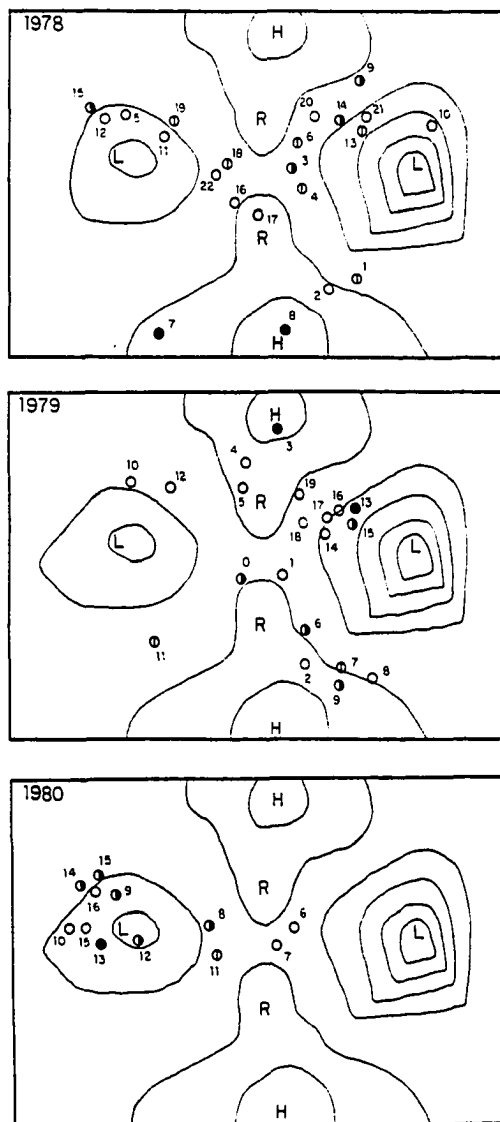


Figure 13. Location of the Copper River Delta, Alaska, on successive days during early autumn 1978, 1979, and 1980 relative to generalized synoptic surface weather features (map from Blokpoel and Gauthier 1980). High (H) and low (L) pressure systems are depicted as well as ridges (R) of high pressure. A weak low is on the left and a strong low on the right. Numbers correspond to dates (1=19 August, 22=10 September). Estimated daily migration volume is indicated by the type of circle: ○ 0-250 geese; ⊙ 250-500; ⊗ 500-1,000; ● >1,000.

14).

B. Relationships with Original Weather Variables

Among all weather variables measured (Table 7), wind was most highly correlated with migration in both spring and autumn, followed by pressure, temperature, and precipitation. Original wind variables (components) were at least as useful predictors as were derived variables such as expected groundspeed. In spring visible migration showed a strong positive correlation with (1) headwinds in the upper air and at the surface near the takeoff point, (2) onshore crosswinds at the surface, (3) barometric pressure, and (4) diurnal range in temperature. Migration was negatively associated with tailwinds, amount and duration of precipitation, and 24-h change in temperature.

In autumn, only wind variables were significantly correlated with migration volume when the entire period was considered. In contrast to spring, observed migration was associated with tailwinds both at the surface at Cordova and in the upper air at Yakutat. Migration was less with NE than SW crosswinds.

C. Multiple Regression Analyses

To avoid "overfitting" in the regression analysis, a phenomenon caused by spurious correlations in analyses using large ratios between the number of predictor variables and the number of cases, I

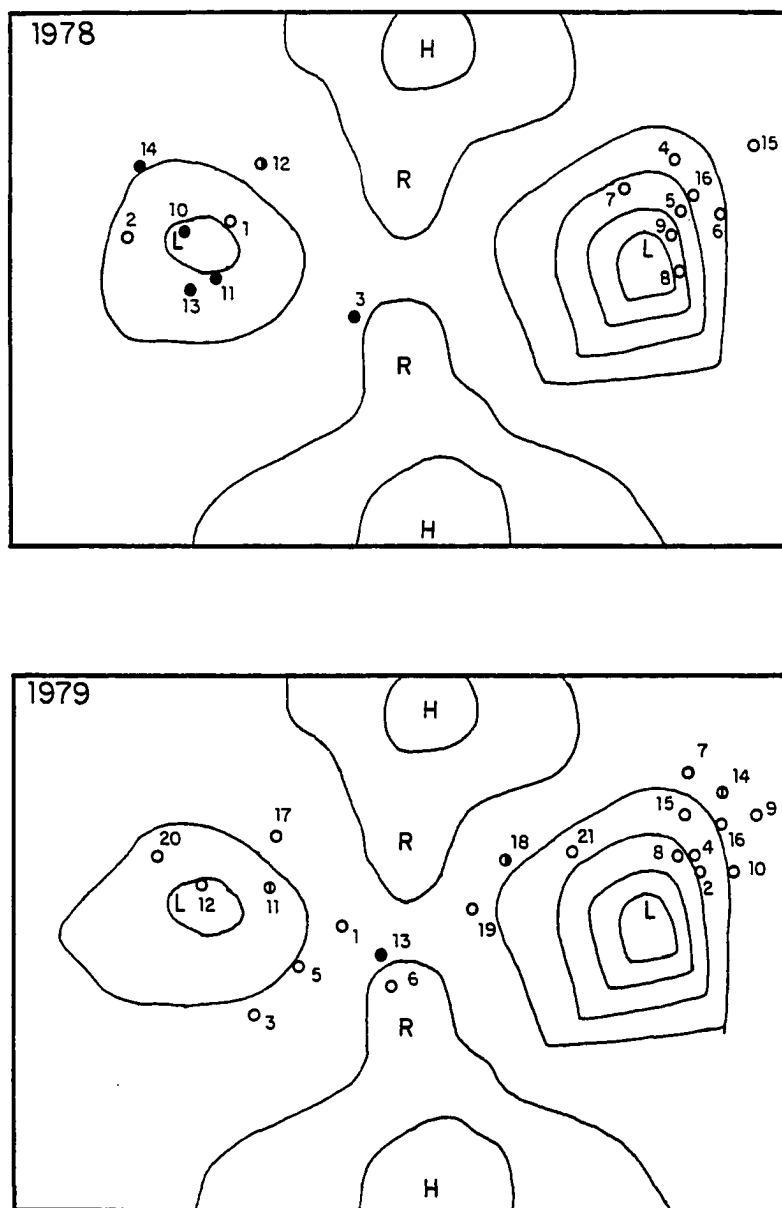


Figure 14. Location of the Copper River Delta, Alaska, on successive days during late autumn 1978 and 1979 relative to generalized synoptic surface weather features (map from Blokpoel and Gauthier 1980). High (H) and low (L) pressure systems are depicted as well as ridges (R) of high pressure. A weak low is on the left and a strong low on the right. Numbers correspond to dates (1=1 October, 21=21 October). Estimated daily migration volume is indicated by the type of circle: ○ 0-600 geese; ⊕ 600-1,200; ● 1,200-2,400; ● >2,400.

Table 7. Weather and temporal variables used in analyses of spring and fall goose migration past the eastern Copper River Delta, Alaska, 1978 and 1979, and their bivariate relationships with the volume of migration.^b

| Variable | Units | Abbreviation | Spring | | | | Autumn |
|--|-------|--------------|-------------|----------------|----------------------|---|---------|
| | | | April & May | | April | | N=31 |
| | | | N=51 | r ^a | N=21 | r | |
| NW(positive)-SE(negative) component(comp) surface(sfc) wind at Cordova(Cdv) 1400 h local time(LT) | km/h | NWCPUSUCO | .20 | | -.23 | | .48** |
| SW(positive)-NE(negative) comp sfc wind at Cdv 1400 h LT | km/h | SWCPUSUCO | .22 | | .66*** | | .43* |
| NW-SE comp 1000 m asl wind at Yakutat(Yak) 1400 h LT | km/h | NWCPUAYA | .10 | | .68*** | | .37* |
| SW-NE comp 1000 m asl wind at Yak 1400 h LT | km/h | SWCPUAYA | .18 | | -.27 | | .09 |
| NW-SE comp 1000 m asl wind at Anchorage(Anc) 1400 h LT | km/h | NWCPUAAN | | | | | .19 |
| SW-NE comp 1000 m asl wind at Anc 1400 h LT | km/h | SWCPUAAN | | | | | .35* |
| NW-SE comp 1000 m asl wind at Yak(spring) or Anc(fall) 0200 h LT | km/h | NWCPUAO2 | | | | | .20 |
| SW-NE comp 1000 m asl wind at Yak(spring) or Anc(fall) 0200 h LT | km/h | SWCPUAO2 | | | | | .00 |
| NW-SE comp sfc wind at Yak(spring) or Anc(fall) 1400 h LT | km/h | NWCPUSU14 | | | .54 ^d * | | -.27 |
| SW-NE comp sfc wind at Yak(spring) or Anc(fall) 1400 h LT | km/h | SWCPUSU14 | | | .58 ^d ** | | .30(*) |
| NW-SE comp sfc wind at Yak(spring) or Anc(fall) 0200 h LT | km/h | NWCPUSU02 | | | .29 ^d | | .12 |
| SW-NE comp sfc wind at Yak(spring) or Anc(fall) 0200 h LT | km/h | SWCPUSU02 | | | .47 ^d * | | -.09 |
| expected(exp) groundspeed(grndsp) along preferred track as a proportion of airspeed (Alerstam 1978:291) based on airspeed of 56 km/h(airspeed of snow geese measured by Blokpoal 1974), based on sfc wind at Cdv 1400 h LT | none | GSURCDV | -.19 | | .27 | | .48** |
| exp grndsp based on 1000 m asl wind at Yak 1400 h LT | none | GUAYAK | -.10 | | -.68*** | | .31(*) |
| exp grndsp based on 1000 m asl wind at Anc 1400 h LT | none | GUANCH | | | | | .13 |
| exp grndsp based on 1000 m asl wind at Yak(spring) or Anc(fall) 0200 h LT | none | GUA0200 | | | | | .11 |
| exp grndsp based on sfc wind at Yak(spring) or Anc(fall) 1400 h LT | none | GSUR1400 | -.07 | | -.58** | | -.30(*) |
| exp grndsp based on sfc wind at Yak(spring) or Anc(fall) 0200 h LT | none | GSURO200 | | | | | .06 |
| 12 h change(chge) in exp grndsp based on sfc wind at Yak(spring) or Anc(fall) 0200 h to 1400 h LT | none | DG12SU | | | | | -.30(*) |
| 24 h chge in exp grndsp based on sfc at Yak(spring) or Anc(fall) 1400 h to 1400 h LT | none | DG24SU | | | | | -.10 |
| 12 h chge in exp grndsp based on 1000 m asl wind at Yak(spring) or Anc(fall) 0200 h to 1400 h LT | none | DG12UA | | | | | -.01 |
| 24 h chge in exp grndsp based on 1000 m asl wind at Yak(spring) or Anc(fall) 1400 h to 1400 h LT | none | DG24UA | | | -.05 ^d | | .03 |
| 12 h chge in NW-SE comp sfc wind at Yak(spring) or Anc(fall) 0200 h to 1400 h LT | km/h | D12NSU | | | .43 ^d (*) | | -.32(*) |
| 12 h chge in SW-NE comp sfc wind at Yak(spring) or Anc(fall) 0200 h to 1400 h LT | km/h | D12SSU | | | .40 ^d (*) | | .32(*) |
| 24 h chge in NW-SE comp sfc wind at Yak(spring) or Anc(fall) 1400 h to 1400 h LT | km/h | D24NSU | | | .11 ^d | | -.10 |
| 24 h chge in SW-NE comp sfc wind at Yak(spring) or Anc(fall) 1400 h to 1400 h LT | km/h | D24SSU | | | .19 ^d | | .21 |
| 12 h chge in NW-SE comp 1000 m asl wind at Yak(spring) or Anc(fall) 0200 h to 1400 h LT | km/h | D12NSUA | | | | | -.06 |
| 12 h chge in SW-NE comp 1000 m asl wind at Yak(spring) or Anc(fall) 0200 h to 1400 h LT | km/h | D12NSUA | | | | | .28 |
| 24 h chge in NW-SE comp 1000 m asl wind at Yak(spring) or Anc(fall) 1400 h to 1400 h LT | km/h | D24NSUA | | | .05 ^d | | .05 |
| 24 h chge in SW-NE comp 1000 m asl wind at Yak(spring) or Anc(fall) 1400 h to 1400 h LT | km/h | D24NSUA | | | .10 | | .11 |
| 24 h chge in NW-SE comp sfc wind at Cdv 1400 h to 1400 h LT | km/h | D24NSCO | .01 | | -.16 | | .06 |
| 24 h chge in SW-NE comp sfc wind at Cdv 1400 h to 1400 h LT | km/h | D24NSCO | -.20 | | -.01 | | .24 |
| 24 h chge in exp grndsp based on sfc wind at Cdv 1400 h to 1400 h LT | none | DG24CO | -.02 | | .15 | | .07 |
| (exp grndsp based on 1000 m asl wind)-(exp grndsp based on sfc wind 1400 h LT) Yak(spring), Anc(fall) | none | DGSUUA | -.06 | | -.25 | | .29 |

Table 7. (continued)

| Variable | Units | Abbreviation | Spring April & May N=51 | | April | Autumn | |
|---|------------------------|--------------|-------------------------------|---|--------|--------|------|
| | | | r | p | r p | N=31 | r p |
| Cloud cover at Cdv: total of values at 0500,1200,1900 h LT..... | 0-30 tenths | CLDCOV | .08 | | -.29 | | .00 |
| Cloud ceiling at Cdv 1200 h LT..... | 1-6 | CLGHT | .02 | | .18 | | .09 |
| 1 -under 500 ft | | | | | | | |
| 2 -600 to 1200 ft | | | | | | | |
| 3 -1200 to 3900 ft | | | | | | | |
| 4 -4000 to 9900 ft | | | | | | | |
| 5 -10000 to 50000 ft | | | | | | | |
| 6 -unlimited(opaque cloud cover less than 6/10) | | | | | | | |
| Visibility at Cdv: total of values at 0500,1200,1900 h LT..... | mi | VSBLTY | -.18 | | .10 | | .09 |
| Daily precipitation at Cdv..... | log ₁₀ (in) | LOGRAINA | -.14 | | -.43* | | .03 |
| Duration of rain at Cdv..... | 1-3 | RAINDU | -.20 | | -.52* | | -.23 |
| 0 - none | | | | | | | |
| 1 - drizzle or occasional light rain("R-" appears up to 9 times) | | | | | | | |
| 2 - rainshowers more frequent("R-" or "RW" appear 10 to 19 times) | | | | | | | |
| 3 - rain continuous("R-" or "RW" appear more than 19 times) | | | | | | | |
| Diurnal temperature range: daily maximum - daily minimum..... | ±°F | MAXMIN | -.04 | | .43* | | .16 |
| 24 h chge in temperature 0500 h to 0500 h LT | ±°F | T0524H | .18 | | .11 | | -.21 |
| 24 h chge in temperature 1200 h to 1200 h LT | ±°F | T1224H | -.35** | | -.45* | | .22 |
| Barometric pressure at Cdv (value - 1000) at 1200 h LT..... | ±mb | PRESS | .35** | | .66*** | | .08 |
| 12 h chge in barometric pressure at Cdv 0000 h to 1200 h LT..... | ±mb | PRECH12H | .14 | | .38(*) | | .20 |
| 24 h chge in barometric pressure at Cdv 1200 h to 1200 h LT..... | ±mb | PRECH24H | .21 | | .14 | | .16 |
| Day spring: 1=16 April, 30=15 May | day | NEDAY | -.47*** | | -.52* | | .04 |
| fall: 1=1 October, 21=21 October | | NEDAYSQ | -.44** | | -.57** | | -.02 |
| (Day) ² | day ² | | | | | | |

Notes: ^aPearson product-moment correlation coefficient with migration volume. ^bMigration volume in all analyses was the logarithm of (estimated passage during 12 h + 10). ^cSignificance levels coded as:(*) .1>P>.05, * .05>P>.01, ** .01>P>.001, *** .001>P. ^dN=19

tried to interpret the results in a conservative fashion, and present only models which I could interpret biologically.

Initially, regression analyses were performed on the entire period chosen for analysis in both spring and autumn (see Methods). In spring, missing values for a number of wind variables necessitated a large reduction in the number of variables used in the analyses. The resulting models (Table 8: spring model 1; autumn) explained little of the variation in migration volume in either season. There were also abnormal patterns in plots of the residuals vs. time, indicating that observed migration was consistently lower than predicted during some periods, and higher than predicted during others. Based on these patterns, similarities in the observed migration between the two years, and previous knowledge (Isleib and Kessel 1973, Petersen et al. 1981, Isleib 1977, D. Timm pers. comm.), further analysis was restricted to a designated "peak" migration period (15-30 April) in spring. This minimized residual variation due to missing time variables, i.e. fluctuations in the intrinsic migration pattern. In autumn, the only such "peak" period evident (10-14 October) was too small to permit further analysis.

The resulting model for April (Table 8, model 2) explained 63% of the total variation in migration volume, though evidence of a missing time variable persisted in the residuals. When the analysis was repeated with first and second order time variables (NEDAY, NEDAYSQ; see Table 7) forced into the equation after the weather variables, this pattern was totally eliminated. This final model

Table 8. Results of stepwise multiple regression analyses of migration volume and weather variables for spring and fall 1978 and 1979.

| <u>SPRING</u> | | | | | | |
|--|----------------|---|-------------|-------------|------------------------------------|--|
| 1. April and May | | Multiple R ₂ = .573 Adjusted R ² = .285 SE of estimate = .698 | | | | |
| Analysis of Variance | | | | | | |
| | Sum of Squares | DF | Mean Square | F | Apparent significance ¹ | |
| Regression | 11.20 | 3 | 3.73 | 7.65 | *** | |
| Residual | 22.92 | 47 | .49 | | | |
| Variables in the Equation | | | | | | |
| Variable | Coefficient(B) | SE of B | Standard B | F to remove | Apparent significance | |
| NW-SE comp sfc wind Cdv 1400 h LT | .036 | .013 | .364 | 7.97 | * | |
| Duration of rain at Cdv | -.250 | .105 | -.296 | 5.63 | * | |
| 24 h chge in temperature 1200 h LT | -.088 | .021 | -.565 | 18.15 | *** | |
| Constant | 3.415 | | | | | |
| 2. April | | Multiple R = .829 Adjusted R ² = .633 SE of estimate = .356 | | | | |
| Analysis of Variance | | | | | | |
| | Sum of Squares | DF | Mean Square | F | Apparent significance | |
| Regression | 4.76 | 3 | 1.59 | 12.50 | *** | |
| Residual | 2.16 | 17 | .127 | | | |
| Variables in the Equation | | | | | | |
| Variable | Coefficient(B) | SE of B | Standard B | F to remove | Apparent significance | |
| NW-SE comp 1000 m asl wind at Yak 1400 h LT | .019 | .005 | .551 | 13.94 | ** | |
| 24 h chge in temperature 1200 h LT | -.061 | .019 | -.448 | 10.69 | ** | |
| Diurnal temperature range | .023 | .013 | .266 | 3.20 | | |
| Constant | 3.183 | | | | | |
| 3. April - temporal variables entered at steps 4 and 5 | | Multiple R = .922 Adjusted R ² = .801 SE of estimate = .262 | | | | |
| Analysis of Variance | | | | | | |
| | Sum of Squares | DF | Mean Square | F | Apparent significance | |
| Regression | 5.89 | 5 | 1.18 | 17.12 | *** | |
| Residual | 1.03 | 15 | .069 | | | |
| Variables in the Equation | | | | | | |
| Variable | Coefficient(B) | SE of B | Standard B | F to remove | Apparent significance | |
| NW-SE comp 1000 m asl wind at Yak 1400 h LT | -.009 | .005 | .267 | 4.24 | | |
| Diurnal temperature range | .034 | .010 | .395 | 11.98 | ** | |
| 24 h chge in temperature 1200 h LT | -.069 | .014 | -.503 | 23.45 | *** | |
| Day | .135 | .062 | 1.003 | 4.73 | (*) | |
| Day ² | -.011 | .004 | -1.399 | 8.60 | * | |
| Constant | 2.786 | | | | | |
| <u>AUTUMN</u> | | Multiple R = .550 Adjusted R ² = .252 SE of estimate = .901 | | | | |
| Analysis of Variance | | | | | | |
| | Sum of Squares | DF | Mean Square | F | Apparent significance | |
| Regression | 9.826 | 2 | 4.913 | 6.06 | * | |
| Residual | 22.684 | 28 | .810 | | | |
| Variables in the Equation | | | | | | |
| Variable | Coefficient(B) | SE of B | Standard B | F to remove | Apparent significance | |
| NW-SE comp sfc wind at Cdv 1400 h LT | .049 | .023 | .372 | 4.76 | (*) | |
| SW-NE comp sfc wind at Cdv 1400 h LT | .034 | .020 | .288 | 2.86 | ns | |
| Constant | 2.738 | | | | | |

Notes: ¹Significance levels are overestimated due to the combination of a large ratio of predictor variables:cases and the criteria used for inclusion of variables in the model.

explained 80% of the variation in migration volume.

In the April and autumn models, a wind variable was the first included. In April the entry of this single wind variable rendered remaining wind variables useless as predictors of additional variation, indicating that those which were most highly correlated with migration volume were intercorrelated with one another. For example, the NW-SE Yakutat upper air wind component had only slightly higher correlation with migration volume than did the SW-NE Cordova surface wind component (Table 7), yet the two were highly intercorrelated ($r=.78$ ***). In contrast, the SW-NE component of surface wind at Cordova was the second most important predictor of late autumn migration, independent of the NW-SE component. Additional variation in migration during April was explained by diurnal temperature range and 24-h temperature change.

D. Factor Analysis of Weather Variables

Hypothetical variables (factors) extracted from the original subset of weather variables were more easily interpreted after non-orthogonal than after orthogonal rotation, and only the results of non-orthogonal rotation are presented (Tables 9, 10). In both seasons the largest proportion of variability in the original variables was accounted for by the inter-correlated effects of precipitation, cloudiness, and diurnal temperature range (Factor 1), all of which indicate "fairness" of the weather. In autumn, several

Table 9. Relationships between spring weather factors derived by Direct Quartimin Rotation and original weather variables after sorting and deletion of correlations (loadings) ± 0.250 .

| Original Variable | Precipitation - cloudiness Factor 1 | Pressure Change Factor 2 | Upper air Headwind Factor 3 | Surface Headwind Factor 4 | SW-NE Component Surface wind Factor 5 | Temperature Change Factor 6 |
|-------------------|--|-----------------------------|--------------------------------|------------------------------|--|--------------------------------|
| RAINDU | 0.964 | 0. | 0. | 0. | 0. | 0. |
| LOGRAINA | 0.932 | 0. | 0. | 0. | 0. | 0. |
| MAXMIN | -0.810 | 0. | 0. | 0. | 0. | -0.261 |
| CLGHT | -0.749 | 0. | 0. | 0. | 0. | 0. |
| CLDCOV | 0.748 | 0. | 0. | 0. | 0. | 0. |
| VSBLY | -0.709 | 0. | 0. | 0. | -0.282 | 0. |
| PRECH24H | 0. | 0.959 | 0. | 0. | 0. | 0. |
| PRECH12H | 0. | 0.926 | 0. | 0. | 0. | 0. |
| NWCPSU14 | 0. | 0. | 0.866 | 0. | 0. | 0. |
| NWCPUAYA | 0. | 0. | 0.849 | 0. | 0. | 0. |
| SWCPSUCO | -0.462 | 0.259 | 0.547 | 0. | 0. | 0.279 |
| D24NCO | 0. | 0. | 0. | 0.925 | 0. | 0. |
| NWCPSUCO | 0. | 0. | 0. | 0.906 | 0. | 0. |
| SWCPSU14 | 0. | 0. | 0.283 | 0. | 0.702 | 0. |
| PRESS | -0.294 | 0. | 0. | 0.255 | 0.666 | 0. |
| D24SCO | 0. | 0. | 0.343 | 0.322 | -0.522 | 0.459 |
| T0524H | 0. | 0. | 0. | 0. | 0. | 0.830 |
| T1224H | 0. | 0. | 0. | 0.281 | -0.273 | -0.467 |
| SWCPUAYA | 0.296 | 0.489 | -0.275 | 0. | 0.322 | 0. |

Table 10. Relationships between fall weather factors derived by Direct Quartimin Rotation and original weather variables after sorting and deletion of correlations (loadings) ± 0.250 .

| Original Variable | Precipitation - cloudiness Factor 1 | SW-NE wind component Factor 2 | Pressure Factor 3 | Surface headwind Factor 4 | Upper air headwind Factor 5 | Surface wind at takeoff point Factor 6 | temperature change Factor 7 |
|-------------------|---|-------------------------------------|-------------------------|---------------------------------|-----------------------------------|--|-----------------------------------|
| VSBLTY | 0.959 | 0. | 0. | 0. | 0. | 0. | 0. |
| CLGHT | 0.879 | 0. | 0. | 0. | -0.271 | 0. | 0. |
| LOGRAINA | -0.863 | 0. | 0. | 0. | 0. | 0. | 0. |
| RAINDU | -0.852 | 0. | 0. | 0. | 0. | 0. | 0. |
| MAXMIN | 0.850 | 0. | 0. | 0. | 0. | 0. | 0. |
| CLDCOV | -0.807 | 0. | 0. | 0. | 0. | 0. | 0.360 |
| NWCPUA02 | 0.558 | -0.259 | 0. | 0. | 0. | 0. | 0. |
| SWCPUAAN | 0. | -0.766 | 0.285 | 0. | 0. | -0.262 | 0. |
| SWCPUAYA | -0.659 | -0.707 | 0. | 0. | 0. | 0. | 0. |
| SWCPSUCO | 0.286 | -0.667 | 0. | 0. | 0. | 0. | 0. |
| PRESS | 0. | 0. | 0.830 | 0. | 0. | 0. | 0. |
| PRECH24H | 0. | 0. | 0.663 | 0. | 0. | 0. | 0. |
| SWCPUA02 | 0. | 0. | 0.654 | 0. | 0. | 0. | -0.258 |
| D24SCO | 0. | -0.533 | -0.643 | 0. | 0. | 0. | 0. |
| D24NCO | 0. | 0. | -0.273 | 0.912 | 0. | 0. | 0. |
| NWCPUSUCO | 0. | 0. | 0. | 0.762 | 0. | 0. | 0. |
| D24NUA | 0. | 0. | 0. | 0. | 0.873 | 0. | 0. |
| NWCPUAAN | 0.451 | 0. | 0. | 0. | 0.683 | 0. | 0. |
| NWCPUSU14 | 0. | 0. | 0. | 0. | 0. | 0.887 | 0. |
| SWCPUSU14 | 0. | 0. | 0. | 0. | 0. | -0.869 | 0. |
| T0524H | 0. | 0. | 0. | 0. | 0. | 0. | 0.895 |
| T1224H | 0. | -0.373 | -0.273 | -0.374 | 0. | 0. | 0.535 |
| PRECH12H | 0. | -0.432 | 0. | 0.310 | -0.450 | 0. | 0. |
| D24SUA | 0. | -0.496 | -0.369 | 0. | -0.487 | -0.283 | 0. |
| NWCPUAYA | 0.280 | -0.381 | 0. | 0.437 | 0. | 0. | 0. |

upper air wind components also loaded on this factor. Various SW-NE wind components clustered on Factor 2 in autumn, but were scattered among factors in the spring. Surface winds near the presumed takeoff point varied independently of other variables in the autumn (Factor 6), in contrast to spring. Due to rapid and extreme pressure changes in autumn as compared to spring, the two pressure change variables constituted a distinct factor (Factor 2) in the spring, but were moderately correlated with upper air and surface winds in the autumn (Factors 2, 3, and 4).

E. Relationships between Weather Factors and Migration Volume

In spring, days of heavy migration were most clearly clumped along Factors 3, 5, and to a lesser extent, 1 (Fig. 15), indicating a positive relationship with fair weather, high pressure, weak to moderate surface and upper air headwinds at the takeoff point, and SW crosswinds rather than NE crosswinds at the surface. The pressure change (2) and temperature change (6) factors were of little use in predicting magnitude of migration. With the exception of one notable day in May, days of heavy migration clustered especially tightly on the plot of Factors 3 vs. 5. Headwinds in the upper air (Factor 3) were far more important determinants of migration than were surface headwinds at Cordova (Factor 4), as evidenced by the plot of these two factors.

In autumn, heavy migration occurred on days having fairly high

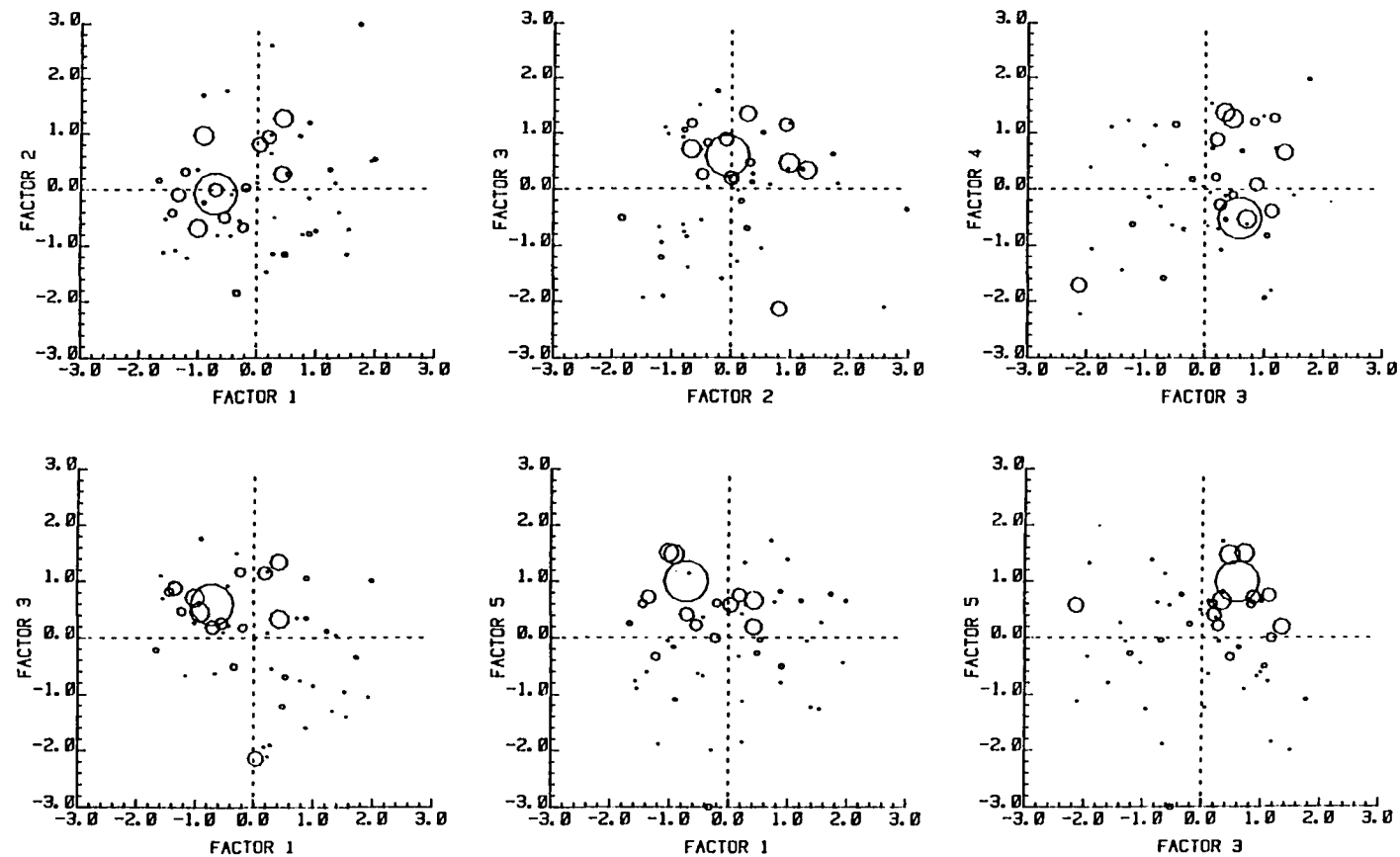


Figure 15. Relationships between daily goose migration through the eastern Copper River Delta, Alaska, and spring weather factors, April and May 1978 and 1979. Each circle represents one day. The sizes of the circles correspond to the amount of estimated 12-h migration (largest = 22,188 geese).

scores on Factors 1 and 4, and low scores on Factor 2 (Fig. 16), indicating a weak positive relationship with fair weather, and a strong positive relationship with tailwinds or weak headwinds in the upper air and at the surface at Cordova, high and increasing SW-NE crosswinds in the upper air and at Cordova, and rapidly increasing pressure. All other factors were of little value. Migration is triggered by rapidly improving weather in the autumn, as evidenced by the correlations of the 12-h vs. the 24-h pressure change variables with Factors 2 and 4 (Table 10).

F. Wind and Visible Migration

The relationships between visible migration and the variables most valuable in describing and predicting it are further depicted in Figs. 17 and 18. In spring, strong winds in the upper air were usually from the SE, and resulted in little visible migration. Heavy migration occurred almost exclusively on days having weak headwinds or calm in the upper air and onshore crosswinds at the surface.

In the late autumn, heaviest visible migration occurred on days having both the most favorable tailwind conditions in the upper air at Anchorage and at the surface at Cordova, and onshore surface crosswinds at Cordova and Yakutat. Apparent exceptions to this were likely either before (2 Oct. 1978) or after (19, 20 Oct. 1979) the main migration period.

In October geese are usually forced to migrate with headwinds or

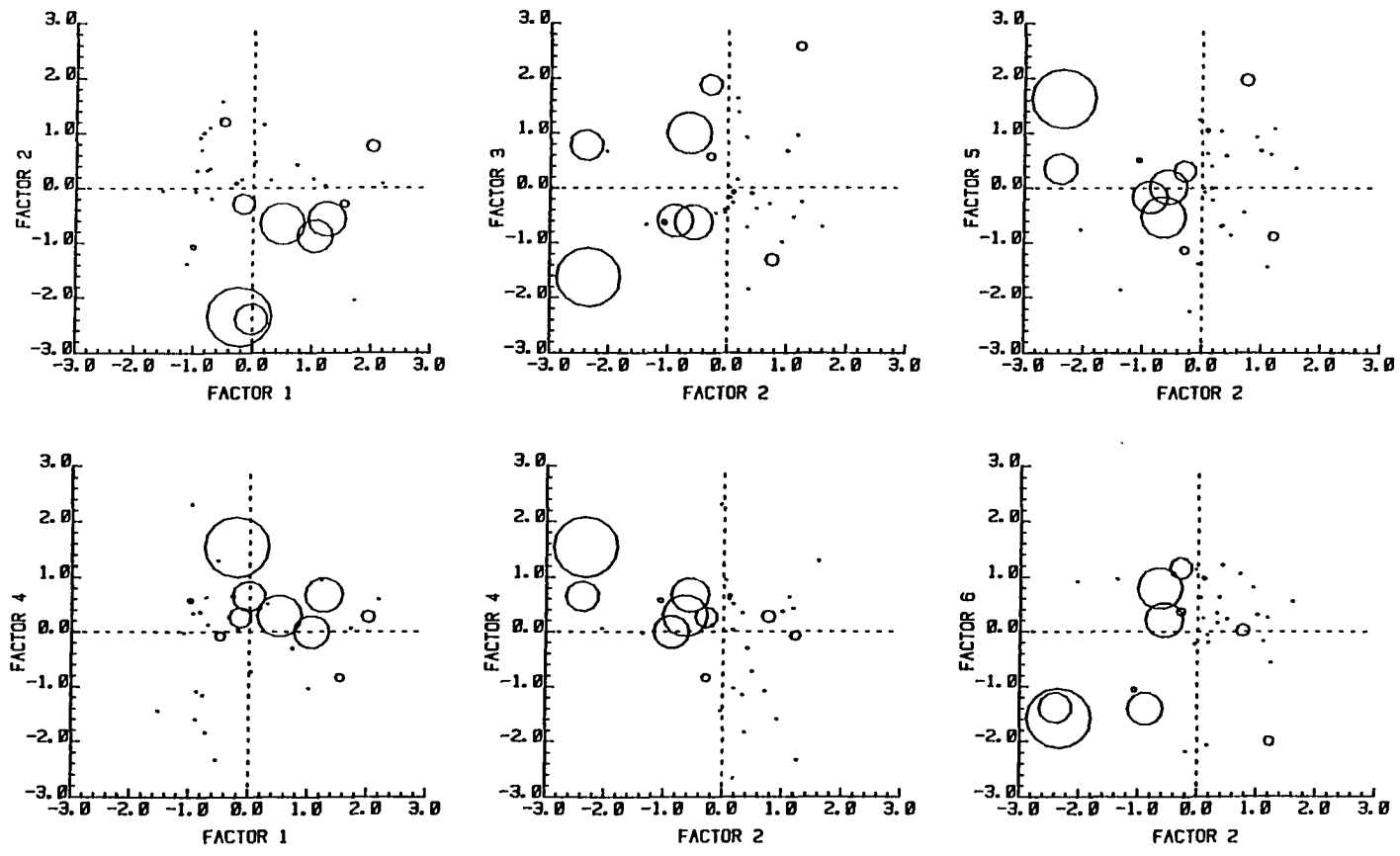


Figure 16. Relationships between daily goose migration volume through the eastern Copper River Delta, Alaska, and autumn weather factors, October 1978 and 1979. Each circle represents one day. The size of the circles corresponds to the amount of estimated 12-h migration (largest=8,136 geese).

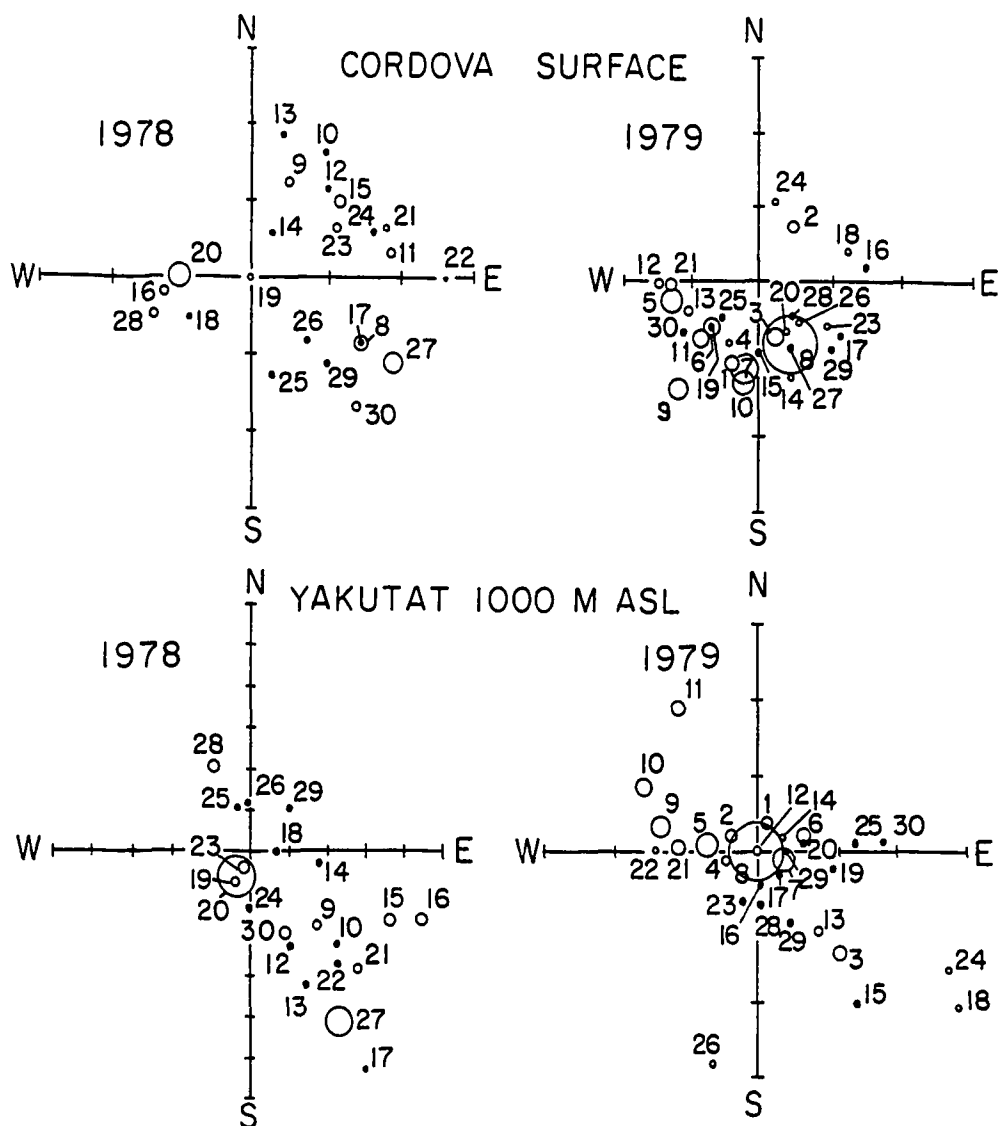


Figure 17. Relationships between daily migration volume and wind speed and direction during spring migration through the eastern Copper River Delta, Alaska, 1978 and 1979. Migration volume is indicated by the size of each circle and numbers correspond to dates (1=16 April, 31=15 May). Position of the circles indicates wind speed and direction; each axis tic mark represents 10 km/h (note that scale is not the same for all sets of axes).

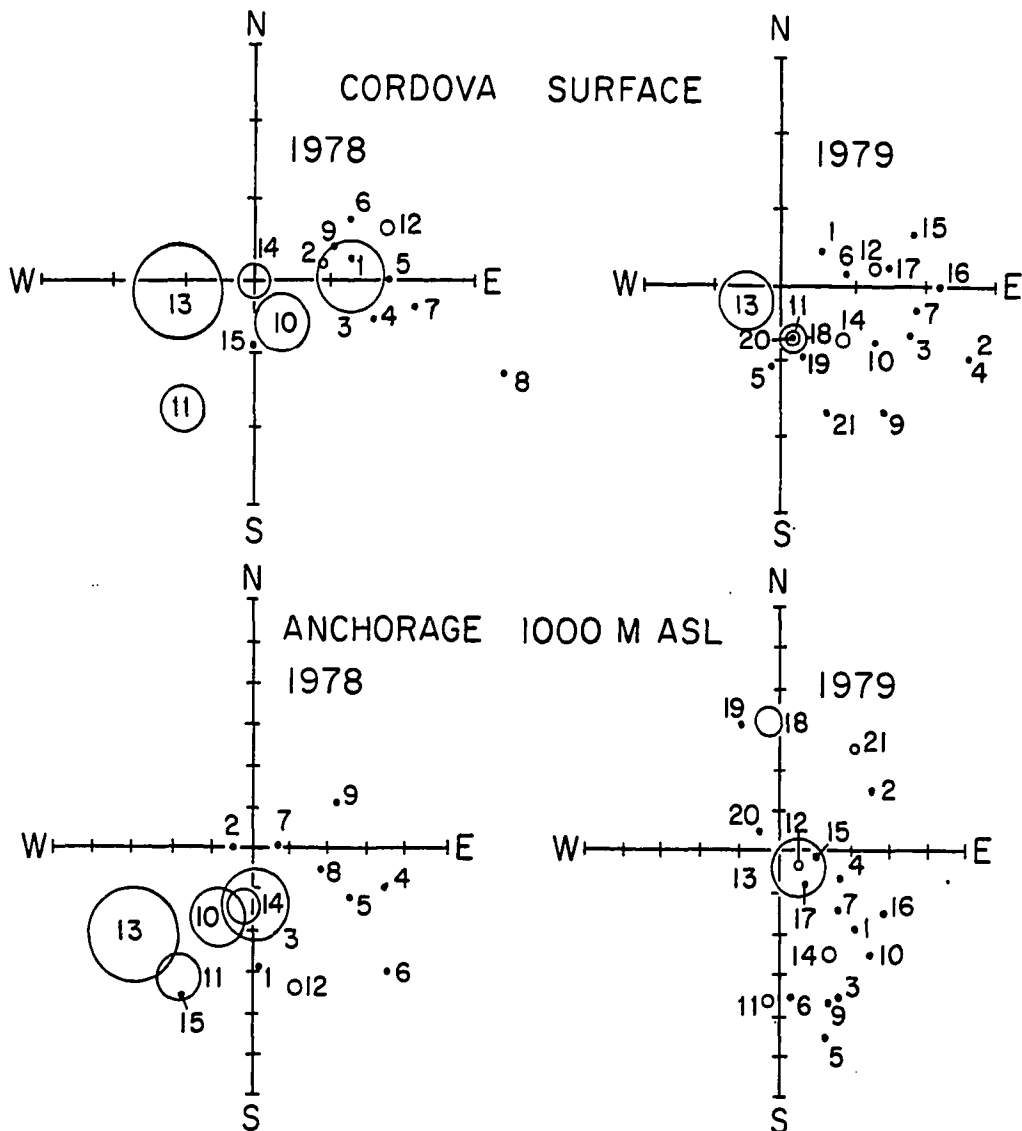


Figure 18. Relationships between daily migration volume and wind speed and direction during late autumn migration through the eastern Copper River Delta, Alaska, 1978 and 1979. Migration volume is indicated by the size of each circle and numbers correspond to dates (1=1 October, 21=21 October). Position of the circle indicates wind speed and direction; each axis tic mark represents 10 km/h (note that scale is not the same for all sets of axes).

crosswinds, since NW winds almost never occur. Occasionally geese initiate migrations under favorable conditions and are grounded en route, sometimes in spectacular concentrations, by rapidly deteriorating weather. Such a situation occurred in 1978. Although habitat use data were not recorded on 7 or 8 October in that year (Fig. 8), at least several thousand B. c. taverneri, several hundred snow geese, and thousands of mallards appeared on the ECRD on the evening of that day accompanied by rapidly increasing E to SE winds (Fig. 18). They had probably departed from upper Cook Inlet that morning under favorable and improving wind conditions, but were forced to take refuge from a rapidly strengthening storm which did not abate until late evening on 9 October. The most impressive autumn concentrations of waterfowl reported in past years on the CRD appear to have followed a similar scenario, in which birds gathered just prior to or during storms, and departed en masse with the return of more moderate weather.

DISCUSSION

I. BEHAVIORAL SIGNIFICANCE OF HABITAT USE PATTERNS

There are at least two possible explanations for the complete switch in feeding habitats by dusky Canada geese during late August/early September: (1) depletion of the food supply in the Saltmarsh, and (2) attenuation of wariness which may have developed during the summer flightless period. I believe that food is depleted in the Saltmarsh during August, to the point that it is no longer energetically profitable for geese to continue feeding there. This results from the combined effects of foraging by the geese, and senescence of leafy plant parts which are a major component of the diet in the Saltmarsh (see Food Habits). Most of the foods consumed in the Freshwater Meadow were storage organs (seeds and below-ground parts).

Observations consistent with the hypothesis that food is significantly depleted in the Saltmarsh during August are as follows:

1. As August progressed, feeding flocks gradually moved from well out in the Saltmarsh to near its upper edge.
2. Preferred food plants in the Saltmarsh were heavily grazed by mid to late August. The leaves of virtually every Triglochin maritimum plant were clipped, often to the ground, and most plants of Plantago maritima had at least several leaves clipped.
3. occidentalis, like other geese, behaved as though they felt most

secure in the Saltmarsh, where visibility is unrestricted by tall vegetation. They seek this habitat for roosting and when harassed by predators (eagles and hunters). During the initial stages of the shift of feeding activities from the Saltmarsh to the Freshwater Meadow, I observed flocks repeatedly hesitate to land in the Freshwater Meadow and eventually return to the Saltmarsh.

Geese have good reason to be nervous in the Freshwater Meadow. In most parts of this habitat hunters can approach close enough to shoot before the geese can detect them through the tall grass and shrubs. B. c. occidentalis feeding in the Freshwater Meadow also appear to have difficulty detecting low-flying eagles; I observed a number of attacks and kills of geese by eagles in which the eagle surprised a flock at fairly close range in the Freshwater Meadow.

There are probably three reasons why B. c. taverneri and C. caerulescens do not use the Freshwater Meadow in the autumn, while B. c. occidentalis do. Firstly, although all three taxa behaved as though they felt more secure in the Saltmarsh, the former two probably have a greater inherent preference for open areas with unrestricted visibility. This follows logically from differences in the characteristics of the breeding habitats they use. The former two are tundra nesters, while dusky Canada geese nest among tall sedges and grasses and an increasing number of shrubs on the WCRD. Behavioral differences similar to these are evident among some subspecies of Canada geese on the wintering grounds in North America

(Marquardt 1962, Grieb 1970:27, Simpson and Jarvis 1979), and between pinkfooted geese and greylag geese in Scotland (Newton et al. 1973).

Observations of Taverner's Canada, cackling, and snow geese feeding in the Freshwater Meadow in spring are not inconsistent with any of the above. In the spring, most of the tall grasses and sedges have been flattened by snow and wind, and there are no leaves on the shrubs. The result is dramatically improved visibility as compared to the autumn, and this probably reduces the birds' aversion to landing and feeding there. Also, in the spring there is no hunting to maintain the wariness geese display during the autumn and early winter.

A second reason why taxa other than B. c. occidentalis do not use the Freshwater Meadow in autumn is that they are physiologically better prepared for migration when they pass through the ECRD than any dusky Canada geese are until at least late September (unpubl. data). Dusky Canada geese probably need to feed intensively during August and most of September to build up sufficient nutrient reserves for migration. Using the resources of the Freshwater Meadow may be the best option for that part of the population which traditionally stages on the ECRD.

Thirdly, the decline in preferred food plants such as Triglochin spp. and Puccinellia spp. which has probably occurred since the uplift has decreased the value of the area to snow, white-fronted, and Taverner's Canada geese, which use those plant species heavily in the saltmarshes of upper Cook Inlet during autumn migration. This is

an effect which would have come into play before the visual deterrent posed by shrubs; the latter has probably only become a significant factor within the last 5-7 years.

Continued succession will result in further deterioration of the Freshwater Meadow as goose habitat. Shrub growth and the loss of preferred food plants have already contributed to the abandonment of this habitat as an autumn feeding area by snow, Taverner's Canada, and most white-fronted geese. I expect these taxa will completely cease any spring use as well within five years or so. Eventually, conditions may become intolerable even for dusky Canada geese.

As the Saltmarsh continues to expand and become more densely vegetated, it should be increasingly used by all goose taxa during both spring and autumn. The rate at which the quality and quantity of this habitat increases will partially determine both (1) the time at which dusky Canada geese completely abandon the Freshwater Meadow, and (2) the rate at which other taxa re-establish a tradition of using the ECRD as a regular stopover during spring and especially autumn migration.

It is fairly clear from differences in past and present vegetation, and from the few historical bird use data, that the ECRD was a more valuable autumn migration area for geese than was the WCRD. It is not clear whether this is still the case or not, since use of the ECRD has greatly declined, and there are few data from the WCRD.

The ECRD will probably regain its comparative value as an autumn

migration area over the WCRD, based on the lack of developing Saltmarshes on the WCRD (personal observation); the only Saltmarsh developing there is composed largely of Carex lyngbyaei, which is not a particularly sought-after food beyond late August. Egg Island, offshore from the WCRD, may be comparable to Strawberry Reef in value, but the existence of Saltmarshes on it has not been documented.

II. FOOD HABITS

A. Comparison with Other Studies

Several Saltmarsh foods which were positively selected by geese in this study, leaves of Puccinellia, Triglochin maritimum, and (to a lesser extent) Plantago maritima, stand out as being highly preferred foods of many goose taxa in both North America and Europe. These are not only important spring, summer, and autumn foods in the subarctic (Quimby 1972, Hanson and Jones 1976:17, Wypkema 1977, Jefferies et al. 1979, Jeffrey and Kaiser 1979, Prevett et al. 1979, Vince 1981, Timm and Sellers 1981), but also during the autumn and winter in more temperate areas such as Britain (Ranwell and Downing 1959; Leisler 1969 in Owen 1971; Owen 1971, 1976; Owen and Kerbes 1971; Charman and Macey 1978). Equisetum spp. and Eleocharis spp. are also frequently mentioned as important natural food items in both North America and Europe (Hanson and Jones 1976:253, Prevett et al. 1979, Palmer 1976,

Owen 1980, McLandress and Raveling 1981, Thomas and Prevett 1982).

There are many references to medium-sized and larger Canada geese feeding on grass seeds, other natural seeds, and various roots during autumn and winter (Palmer 1976, Bellrose 1976), presumably as they did before the advent of modern agriculture. The importance of below-ground storage parts as traditional foods for snow geese (Palmer 1976, Jeffrey and Kaiser 1979, Prevett et al. 1979, Smith and Odum 1981), and white-fronted geese (Pollard and Walters-Davies 1968, Palmer 1976, Owen 1976) is also documented. The use of sedge shoots by geese in spring is a widespread phenomenon (e.g. Hanson 1962).

Arrowgrasses (Triglochin spp.) appear to be an extremely important natural food of geese. Although T. maritimum is not an abundant plant on the ECRD, it is ubiquitous in the extensive saltmarshes of Cook Inlet, Alaska (Hanson 1959, Quimby 1972, Sellers 1979, Timm and Sellers 1980, Vince 1981), Hudson Bay (Prevett et al. 1979, Ringius 1980), and is at least common in other saltmarshes of the North Pacific Coast (e.g. del Moral and Watson 1978, Jeffrey and Kaiser 1979), as well as those of the British Isles and Scandinavia. Throughout these areas the leaves and occasionally seeds (Quimby 1972, Thomas and Prevett 1981) are sought by a variety of geese (Charman and Macey 1978, Prevett et al. 1979, Jeffrey and Kaiser 1979, Owen 1980, Timm and Sellers 1980) during all seasons of the year.

Triglochin palustris is also a widespread species (Hulten 1968), but the importance of its bulbs to geese has only recently been

discovered (Prevett et al. 1979, Thomas and Prevett 1981, Timm and Sellers 1980). These are used both in autumn and spring, and are also used by other animals. Herter (1982) found that sandhill cranes feed almost exclusively on this food during the autumn and spring migrations on the ECRD. Brown bears (Ursus arctos) also eat T. palustris bulbs during the autumn on the ECRD.

The excellent nutritional value of the seeds of T. maritimum and bulbs of T. palustris has recently been documented (Thomas and Prevett 1981, Herter 1982).

B. The Significance of Food Selectivity

Geese have repeatedly demonstrated their adaptability to changes in habitat and thus food sources. Many studies of foraging and food selection by geese have concluded that they feed in such a way as to maximize their net intake of energy and certain nutrients. They are able to distinguish fertilized vegetation and concentrate grazing efforts on fertilized areas (Lieff 1973; Harwood 1975, 1977; Owen 1975; I. Valiela, Marine Biol. Lab., Woods Hole, MA., unpubl. data), even when humans cannot visually distinguish which areas are fertilized (Owen 1975, Owen et al. 1977). Several studies of grazing have concluded that geese were maximizing their intake of protein by using some correlated cue(s) in the vegetation, such as water content. Possibly this is done by monitoring the tensile strength of leaves, which is negatively correlated with water content and

positively correlated with fiber content (Owen 1976). Fiber lowers the digestibility of food in geese (Nehring and Nerge 1966 in Ebbinge et al. 1975), especially since geese are unable to digest cellulose (Marriot and Forbes 1970, Mattocks 1971). Studies of preference involving other foods such as seeds (McFarland and George 1966), and some winter grazing studies (Owen 1976) suggest that it is the actual nutritive value and probably digestibility rather than protein per se which is correlated to preference. In spring and summer grazing, digestibility happens to be positively related to protein content, whereas at other times of year preferred foods have the most digestible energy, and probably an adequate supply of protein as well. As an example, geese have been enticed from protein-rich grassland in spring to feed almost exclusively on energy-rich grain, which presumably also provided adequate protein (Owen 1980).

Thus it seems that the tendency of many goose taxa to feed almost exclusively on green leaves in the summer, and a mixture of leaves and storage organs (seeds and roots) in spring and autumn, is adaptive in terms of their seasonal energy needs. Fat and protein reserves are necessary in the spring for migration and nesting activities (Blem 1967; Ankney 1974, 1977; Ankney and MacInnes 1978). During the summer protein is in high demand for the growth of feathers of adults and structural growth of young. In the autumn feather growth must be completed by all age classes, young must complete structural growth, and all must deposit fat for autumn migration (Wypkema 1977, Wypkema and Ankney 1979).

What are the implications of observed diet and habitat use patterns on the ECRD? It appears that a segment of the B. c. occidentalis population is able to complete the final stages of annual molt and accumulate a significant amount of fat (unpubl. data) for migration by feeding on the ECRD from mid August to late September or early October. The observed switch from leaf material in August to carbohydrate-rich seeds (MacLandress and Raveling 1981) and roots in September and October, and the consumption of a mixture of storage and growing parts in spring, is expected based on nutritional requirements. Equisetum appears to be an exception to this rule. Possibly leaves and shoots of this genus contain high levels of some essential nutrients not available in other foods during late summer and autumn. At James Bay, where this genus is an important spring, summer, and autumn food of geese, the rhizome tips and aerial stems were found to contain high levels of protein in spring and summer, and somewhat lower, but possibly still high relative to other foods, levels in autumn (Thomas and Prevett 1982). Stelmock (1981) found that above-ground parts of this genus were an important food for grizzly bears during spring and summer, and that they had high protein content and high digestibility.

Judging from the variety of plants and plant parts eaten in the Saltmarsh and the Freshwater Meadow, it seems that the adaptability of "intermediate-sized" Canada geese to a variety of foraging modes (grazing, stripping seeds, digging for roots; Reed 1976) is being fully utilized during autumn by dusky Canada geese on the ECRD. An

unanswerable, but important question is whether these birds are able to forage as efficiently now as they did prior to the earthquake, when they probably fed exclusively in Saltmarsh habitat.

III. THE INFLUENCE OF WEATHER ON MIGRATION

A. Migration Behavior of Geese in Relation to Weather

In the analyses of migration volume vs. weather most of the variation in visible migration not attributable to the intrinsic migration pattern has been explained by weather variables. An explanation of the actual behavior of migrants which is consistent with these relationships is now offered. The explanation is based on the premise that migrating birds will choose routes and altitudes which offer the highest groundspeed along the preferred track with the least expenditure of energy (Alerstam 1978).

Several characteristics of wind and pressure systems are critical to understanding the patterns of visible migration. First, surface winds tend to be much weaker than those in the upper air (i.e. 1,000 m asl); this difference is greater over land than sea, and greater over mountainous than flat terrain. Second, surface winds at 60 degrees N are directed an average of 37 degrees counterclockwise from geostrophic winds over land, and 13 degrees over the sea (Godske et al. 1957 in Alerstam 1978). Pressure systems, especially lows, tend to remain stationary in the Gulf of Alaska, or

move E or NE (Brower et al. 1977), weakening as they move onshore. Lows in the Gulf of Alaska bring clouds, rain, and brisk E to SE winds to the North Gulf Coast, while high pressure systems bring fair weather and lighter winds from the SW, W, or NW. In April, 60% of occasions with SE or S winds are characterized by cloud cover greater than 7/8 with bases less than 2,440 m (8,000 ft) asl, but less than 25% of occasions with SW winds have any associated cloud cover (Brower et al. 1977). Similar relationships exist in October.

In the spring, low pressure systems centered in the Gulf of Alaska (e.g. Fig. 19), such as persisted in 1978, provide almost perfect tailwinds for migrants near the coast. Most geese and other birds probably fly over the clouds in these circumstances, thereby taking advantage of stronger tailwinds and less turbulence and less precipitation. Most migrants bypass the CRD and continue to the marshes of Cook Inlet. Highs in the Gulf of Alaska in spring (e.g. April 1979) provide weak opposing winds in the upper air and at the ocean surface, but more favorable tailwinds or onshore crosswinds along the coast. Thus migrants concentrate at low altitude along the coast under such conditions. On such days in April 1979, many birds passed the ECRD within a few m of the water or ground. Most visible migrants were at altitudes of less than 300 m, even when skies were clear.

On an unusual spring day (28 April 1979) when partially clear skies coincided with tailwinds in the upper air, flocks were seen at altitudes as high as 2,000 m, and several were heard migrating over

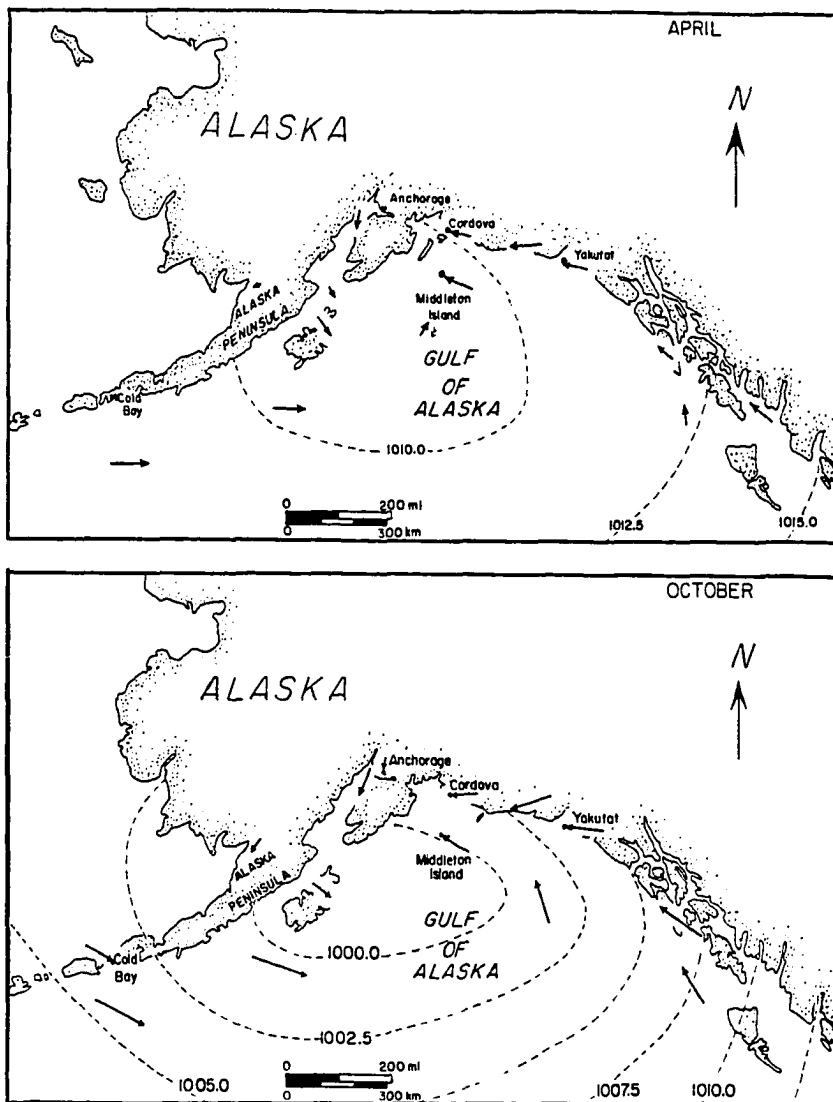


Figure 19. Average sea level barometric pressure and wind patterns in the Gulf of Alaska during April and October. Isobars (dashed lines) are in mb. Arrows depict mean wind speed and direction (largest = 15.4 km/h). Data from Brower et al. (1977).

clouds later in the day. Sandhill cranes were also heard migrating over clouds on this day. Geese were heard above the clouds on 23 April 1979 as well, a day that had very weak winds both at the surface and in the upper air.

Because the two springs of the study had greatly different prevailing weather conditions during April, each may have presented a confusing picture if examined alone. Together, they support the preceding explanations. The suggestion that the majority of migration may occur over clouds in some springs is contradictory to the findings of most radar studies that generally migration is less with clouds and precipitation than with fair skies (Richardson 1978). However, the only other plausible explanation for the paucity of visible migration in 1978 (and in 1980, D. Herter pers. comm., Petersen et al. 1981) is that migration occurred at low altitude offshore. Available evidence does not support this explanation. Data collected in spring of 1977 and 1978 at the southern tip of Kayak Island, 75 km S of the ECRD, indicated little or no visible migration of geese other than brant in either year, and coastal migration was offered as an explanation (Arneson 1978, 1980). Migration of waterfowl and other birds over clouds has been documented previously (Jogi 1960, Bellrose 1967, Blokpoel and Burton 1975), and is especially conceivable along the North Gulf Coast because clouds are usually low and stratiform: in April, 41% of all days have ceilings less than 1,067 m (3,500 ft) at Cordova (Brower et al. 1977). Thus, migrants probably do not need to climb to great altitudes to be above

the clouds, out of turbulence and precipitation. Here they also have access to celestial cues to navigation, which may be critical to birds flying over long stretches of open water (Alerstam and Pettersson 1977, Alerstam 1978).

In October, fairly deep (965-980 mb) lows (Fig. 19) move successively across the Gulf of Alaska, causing persistent E to SE winds in the upper air near the coast. During this month, migration occurs almost every time upper air winds weaken and switch to the SW or NE. These are the most favorable winds which occur with regularity; NW winds are infrequent near the coast in October (Brower et al. 1977). When these weakening winds have an onshore (SW) component, the coast acts as a leading line along which migrants concentrate (e.g. 1978), but when they have an offshore (NE) component, the migration occurs on a broad front extending from the coast over the Gulf of Alaska (e.g. 1979). This front frequently extends far out to sea, as was demonstrated in the autumn of 1980, when mass migration occurred on the same day (10 Oct.) on the ECRD and Middleton Island, 100 km to the SSW (D. Herter pers. comm., Tobish 1980).

Persistent weather patterns in the Gulf of Alaska also offer an explanation for coastal or nearshore migration by many brant, cackling Canada geese, and some shorebirds in the spring vs. largely trans-Gulf migration in the autumn (e.g. Nelson and Hansen 1959, Gill 1978, Gill and Jorgenson 1979, Gill et al. 1979, Isleib 1979, Senner 1979). Myres (1972) observed almost continuous movement of radar

echos over inshore waters parallel to the coastline of southern British Columbia during spring 1965, but now concludes (pers. comm.) that the only echos moving on a trans-Gulf heading were due to sooty shearwaters (Puffinus griseus). By carefully timing trans-Gulf departures from the Alaska Peninsula in autumn, many birds can take advantage of tailwinds on the W side of the same systems which provide tailwinds along the coast in spring. Salomonsen (1967 in Braun 1980) suggested that wheatears (Oenanthe oenanthe) behave in a similar fashion, crossing the North Atlantic Ocean along a more southerly route in autumn than spring to take advantage of a persistent low which exists south of Iceland at about 55 degrees N. Beason (1980) suggested that prevailing wind directions at 60 degrees vs. 45 degrees N were responsible for the clockwise orientation of autumn migration in the SW United States relative to the reverse azimuth of spring migration.

B. Comparison with Other Studies

My findings are consistent with previous studies of goose and other bird migration, both visible and radar-detected, which have found wind to be the most important proximate parameter influencing the timing and amount of migration (Ulfstrand 1960, Blokpoel et al. 1975, Alerstam 1978, Blokpoel and Richardson 1978, Richardson 1978, Blokpoel and Gauthier 1980). However, if selection of optimal wind conditions is actually occurring, as hypothesized in the preceding

section, the actual spring goose migration along the North Gulf Coast may be positively correlated with cloud cover and possibly precipitation in most years, in contrast to the findings of virtually all radar studies of migration (Richardson 1978). Still, this seems plausible in view of the rapidity with which spring migration tends to occur, and the consequences from both an energetic and temporal standpoint, of birds waiting five days or even a week to migrate with less cloud, but also less favorable winds, possibly even headwinds. Time is a factor which probably plays a greater role than either wind or fair weather in this spring migration, since highly unfavorable winds seldom occur, and moderately unfavorable winds are associated with fair weather.

Although unquantified biases in this study, caused by clouds and wind in the spring and crosswinds in the autumn, preclude direct comparison with other studies, observations in both spring and autumn were consistent with previously developed theories about the relationships between wind and visible migration of waterbirds along coastal leading lines (Jogi 1960; Ulfstrand 1960; Bergman 1974, 1978; Alerstam 1978): observed migration was more intense with onshore than offshore crosswinds, and migration was more intense at low altitude along the coast under weak opposed winds than with tailwinds.

Comparisons can be made to a recent visible migration study conducted at Yakutat during spring and autumn 1980 (Petersen et al. 1981), which commented on the relationships between migration and synoptic weather patterns. They concluded that in spring some taxa

migrated with strong tailwinds and others with weak headwinds. However, this discrepancy is probably due to a failure to consider migrants' response to winds at higher altitude. Virtually all the days on which they observed the heaviest migration had synoptic conditions conducive to either strong crosswind components or weak headwinds in the upper air, and weaker, more favorably directed surface winds along the coast. Both of these situations should result in coastal low altitude migration. The former conditions (very strong upper air winds from the S or SW caused by deep lows to the W) occurred infrequently during spring migration in 1978 and 1979, but may explain the heretofore anomalously large visible migration on at least one day on which there was a strong upper air tailwind component accompanied by substantial crosswinds. This day appears as an outlier in the plots of spring weather factors vs. migration volume (Fig. 15, e.g. Factors 5 vs. 3).

In autumn 1980, visible migration of geese and whistling swans past Yakutat appears to have been associated with weakening lows moving onshore, but detailed wind conditions and the dynamics of winds and pressure systems were not reported.

CONCLUSIONS

I. VALUE OF THE ECRD RELATIVE TO OTHER MIGRATION AREAS

It is difficult to compare use of the ECRD with use of other migration areas on the North Gulf Coast and in Cook Inlet because there is little information on use of these other areas during migration. Most current knowledge is from aerial surveys, which were not an integral part of the ECRD study. Use of the Yakutat area has recently been documented, however (Petersen et al. 1981, Patten 1981). At present the Yakutat area appears to be considerably less important than the ECRD to migrating geese, with the likely exception of snow geese. Aside from 11,700 snow geese in the Blacksand-Ahrnklin Estuary on 10 October and 2,308 on 14 October 1980, relatively few geese were observed in the Yakutat area during migration despite intensive and extensive aerial and ground surveys and migration watches in both spring and autumn of 1980. In autumn particularly, many geese passing through the CRD apparently strike out across the Gulf of Alaska and completely bypass the Yakutat area. At least several thousand snow geese gather on the Stikine Delta in Southeast Alaska each autumn, and would be expected to follow the coastline to reach that area.

The little evidence available indicates that Cook Inlet saltmarshes are presently far more important to migrant geese (other than dusky Canada geese) in both spring and autumn than either the

C-BRD system or the Yakutat area. Cook Inlet saltmarshes are both extensive and replete with preferred goose foods (see Hanson 1951, Quimby 1972, Sellers 1979). These marshes host (1) virtually an entire subpopulation of lesser snow geese in the spring and probably autumn; (2) single concentrations of up to 10,000 white-fronted geese in recent years; and (3) spring and autumn congregations of Taverner's Canada geese which occasionally exceed several tens of thousands. Thousands of cackling Canada geese may also pause briefly there during spring migration.

In both spring and autumn, taxa other than B. c. occidentalis have demonstrated that they are not obligate users of the C-BRD system. I suggest that they do require upper Cook Inlet marshes in both seasons for at least several days of resting and feeding before/after long flights along the North Gulf Coast or across the Gulf of Alaska.

II. THREATS TO MIGRANT GEESE IN THE C-BRD SYSTEM

Owing to a multitude of unique wildlife and other natural resource values, the ECRD and the entire C-BRD system are already well-protected by a combination of two cooperative agreements among state and federal agencies (Copper Delta Game Management Agreement, Bering River-Controller Bay Trumpeter Swan Management Area Cooperative Agreement), and the designation of the CRD as Critical Habitat by the State of Alaska. Virtually the entire system is part

of the Chugach National Forest, and the U. S. Forest Service has thus far made every effort to maintain its pristine qualities.

The greatest immediate threat to migrant geese, as well as other organisms using marine and intertidal habitats, is from oil pollution in the Gulf of Alaska. Huge tankers regularly ply the waters offshore from the C-BRD en route to and from the terminus of the Trans-Alaska Pipeline at Valdez. An oil spill could affect the single most important habitat for migrant geese -- saltmarshes, and thus affect migrants either indirectly by reducing or eliminating their food supply, or directly via oil ingestion or fouling of plumage.

Development of timber, petroleum, and coal resources appears increasingly likely in the Martin River and Bering River-Controller Bay areas, including construction of a lateral spur road from the Copper River Highway and a port facility. Again, alteration or destruction of habitat is the greatest danger presented by these potential developments; geese will probably habituate to most temporary or even permanent development-related activities which do not pose an immediate threat to their safety. Aircraft disturbance is a potential danger associated with this development. Judging from the reactions of geese on the ECRD, fixed-wing aircraft pose little problem, but helicopters should be used with caution; dusky Canada geese appear to be least sensitive to aircraft disturbance, and snow geese most sensitive.

There are no significant man-related disturbances to migrating geese in the C-BRD system at present because the area is relatively

inaccessable and no longer offers outstanding waterfowl hunting, as it did prior to the earthquake. This is likely to change either if the hunting improves (as more birds use the developing saltmarsh), or if access is improved (e.g. due to completion of the Copper River Highway).

Cook Inlet marshes presently receive much more intensive use due to their proximity to the population centers of Anchorage and Kenai and the high quality hunting that they offer. Aircraft harassment is already a concern in some of these saltmarshes, but the magnitude of the disturbance is unknown (D. Timm pers. comm., Sellers 1979). Hunting pressure in some areas may also be unduly high, and there may be a need for either aircraft restrictions, designation of sanctuaries, or both.

RECOMMENDATIONS

Regarding the present situation on the ECRD, there is no need for additional regulations or other action to protect either geese or their habitat. Hunting pressure is light (less than 200 hunter-days/year) and disturbance minimal. Routine fixed-wing aircraft traffic associated with the salmon gillnet fishery has no discernable disruptive effect on the activities of geese, particularly dusky Canada geese, which are probably the only obligate users of the area in autumn. All that is necessary is that natural succession be allowed to continue, and the ECRD will eventually regain its status as a migration area.

Within the C-BRD system, I recommend the following research to further understanding of the present and potential value of the area to migrating geese:

1. Periodic monitoring of autumn habitat use on the ECRD, possibly by means of two or three aerial surveys during August and September every few years, to determine if and when use of the Freshwater Marsh discontinues.
2. Quantification of the expansion of saltmarshes throughout the C-BRD lagoon system by means of permanent reference plots, including studies of siltation rates, changes in plant communities, and their relationship to tidal inundation and

salinity. Low level aerial photography of the Freshwater Meadow and Saltmarsh is recommended every 5 years.

3. Migration and habitat use studies in the Bering River-Controller Bay area, since (1) present use is virtually unknown, and (2) future development activities are most likely to be concentrated there. This area is the first part of the system reached by spring migrants, and the probable point of departure for autumn migrants. Migration studies at Okalee Spit or Cape Suckling would monitor definite arrivals of birds in the spring and departures in the autumn, thus avoiding "noise" caused by local movements of birds, a problem evident in the ECRD study and the U. S. Fish and Wildlife Service migration watches at Mummy Island, Orca Inlet.

4. A combined visual and radar migration study at either end of the C-BRD system would provide a wealth of information about trans-Gulf migration and also answer the difficult question of the extent of migration over the clouds.

I also recommend site-specific habitat use and migration studies at several of the Cook Inlet marshes, particularly Redoubt Bay, Susitna Flats, and Chickaloon Flats, and also on the north side of the Alaska Peninsula at Pilot Point. Goose use of these areas is poorly documented, and disturbance of large concentrations of birds

by aircraft and hunters should be assessed.

Another potentially heavily used area about which little appears to be known is the Queen Charlotte Islands; saltmarshes there may be used during spring and autumn migration by both trans-Gulf and more coastal migrants.

SUMMARY

Field studies of timing and amount of migration, habitat use, and food habits of migrating geese were conducted on the eastern portion of the Copper River Delta (ECD), Alaska, during spring and autumn of 1978 and 1979, and early autumn of 1980. Techniques employed were visual migration watches, censuses in selected habitats, collection of geese and collection of samples from hunter-killed birds, systematic vegetation sampling, and general observation. The relationship of weather to visible migration was also examined using descriptive, bivariate, and multivariate analyses.

Five goose taxa (Branta canadensis occidentalis, B. c. taverneri, B. c. minima, Anser albifrons frontalis, Chen caerulescens) were common or abundant during spring migration, and all of these except B. c. minima during autumn migration. Branta bernicla nigricans was uncommon during spring migration. B. c. parvipes and A. a. gambelli undoubtedly passed in spring and autumn, but were both uncommon and difficult to identify.

Spring migration was underway by 14 April and continued until ca. 15 May, with peak numbers passing during 20-30 April. Each taxon appeared to have its own migration rhythm, which was evident during sustained fair weather, but partially obscured when weather was poor or fluctuating. Canada goose subspecies in particular had well-defined, but overlapping, migrations; the largest in body size

were the earliest migrants, and the smallest were the latest. B. c. taverneri was the most abundant taxon in spring.

Autumn migration (ca. 5 August to at least 20 October) was more extended and diffuse than spring migration. B. c. occidentalis passed during August and again in late September and early October. B. c. taverneri migrated in small numbers in late September and in spectacular but sporadic mass migrations after early October. A. albifrons regularly passed in a relatively small pulse during late August and early September.

B. c. occidentalis which migrate through the ECRD nest on the western Copper River Delta (WCRD); B. c. parvipes in Cook Inlet and possibly forested areas of Interior Alaska; and B. c. minima on the Yukon-Kuskokwim Delta. B. c. taverneri passing in spring may be destined for a number of nesting areas in western Alaska, but those passing in autumn probably come from the Kotzebue Basin or Innoko River areas. A. albifrons are probably from Cook Inlet, Bristol Bay, and adjacent inland areas. C. caerulescens nest on Wrangel Island, Siberia.

Virtually all goose use of the ECRD occurred in two habitats: Saltmarsh, which is tidally influenced, has sparse growths of halophytic plants, good visibility, and no shrubs; and Freshwater Meadow, which is above tidal influence and characterized by complete vegetative cover by a wide variety of halophytes and non-halophytes, including large moss-dominated areas. It has widespread shrubs up to 4 m tall, and poor visibility.

Relatively few migrants used the ECRD during spring migration, and those that did usually stayed less than one day, except for some B. c. occidentalis. Saltmarsh was the most frequently used habitat in spring, but several taxa also used the Freshwater Meadow.

In autumn, flocks of B. c. occidentalis intensively used first the Saltmarsh, then Freshwater Meadow, from early August to early October. Individuals stayed on the ECRD as long as 30 days, and the same segment of the population may have been present from late August to late September. Other taxa made little use of the ECRD, and used only the Saltmarsh.

Dusky Canada geese ate at least 26 species of plants of 18 families in the autumn. Equisetum arvense, Triglochin palustris, and Carex lyngbyaei were the three most important foods determined on either a volumetric or frequency and occurrence basis. Leaves and shoots of Equisetum and various halophytes were the predominant foods in the Saltmarsh. Leaves and shoots of Equisetum and various seeds and below-ground storage organs of other taxa were predominant foods in the Freshwater Meadow. Geese selected certain plants and completely avoided others. In spring most geese ate shoots of various monocots, particularly Carex.

The Freshwater Meadow of the ECRD was a saltmarsh prior to the ca. 2 m uplift caused by the 1964 Alaska Earthquake. The uplift completely eliminated tidal influence, and heavy rains leached salts from the soil. This substrate has been invaded by mosses and a variety of grasses, forbs, and shrubs, which continue to thrive at

the expense of the the few residual halophytes. The present Saltmarsh has developed in the last 10 years on the exposed intertidal midflats, and continues to expand.

In spring, visible migration was heaviest when high pressure systems dominated the CRD area, bringing SW surface winds and NW upper air winds, high pressure, clear skies, and large diurnal range in temperature.

In late autumn, heavy migration was associated with the most favorable upper air winds at Anchorage and surface winds at Cordova, SW (onshore) winds in the upper air and at the surface, and rapidly increasing pressure. These conditions result when low pressure systems in the Gulf of Alaska weaken and move onshore west of the CRD. Autumn migration was weakly correlated with fair weather.

The ECRD is an important staging area at present only for B. c. occidentalis, especially in the autumn. For other goose taxa, the C-BRD system is at present probably less important than Cook Inlet marshes, and more important than the Yakutat area in both spring and autumn. The C-BRD system, particularly the ECRD, was a heavily used migration area in both spring and autumn prior to the earthquake, and if successional trends continue, it probably will be again, owing to its location on a major migration corridor.

Threats to the ECRD are few. Use of Cook Inlet marshes, Pilot Point, and the Queen Charlotte Islands should probably be the highest priority for future goose migration studies, but changes in the Saltmarsh and Freshwater Meadows of the C-BRD system should be

reassessed periodically. Site-specific studies in the Bering River Delta-Controller Bay area are advisable in view of impending development activities there.

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Appendix IA. Parameters of daily spring migration watches during 1978 and 1979 on the eastern Copper River Delta, Alaska.

| Date | 1978 | | | | 1979 | | | |
|----------|---------------|---|-------|-----------------|---------------|---|--------|-----------------|
| | Obs. Hours | Net ^a Geese N ₁ /12hrs. | | SE ₁ | Obs. Hours | Net ^a Geese N ₁ /12hrs. | | SE ₁ |
| April 16 | | | | | .5 | 2 | 4392 | 2556 |
| April 17 | | | | | 2.0 | 8 | 4092 | 1728 |
| April 18 | | | | | 2.0 | 8 | 6096 | 2376 |
| April 19 | | | | | 2.0 | 8 | 1656 | 900 |
| April 20 | | | | | 2.0 | 8 | 10164 | 5040 |
| April 21 | | | | | 1.75 | 7 | 7320 | 3468 |
| April 22 | | | | | 1.5 | 6 | 9564 | 2016 |
| April 23 | 1.5 | 6 | 3876 | 2688 | 1.5 | 6 | 22188 | 11100 |
| April 24 | 1.75 | 7 | 1140 | 756 | 2.0 | 8 | 8436 | 5172 |
| April 25 | 2.0 | 8 | 408 | 216 | 1.75 | 7 | 7272 | 3756 |
| April 26 | .75 | 3 | 2412 | 1356 | 1.5 | 6 | 7092 | 3876 |
| April 27 | 1.75 | 7 | 300 | 396 | 1.75 | 7 | 3912 | 1068 |
| April 28 | 1.25 | 5 | 240 | 312 | 1.75 | 7 | 2376 | 1068 |
| April 29 | 2.0 | 8 | 228 | 192 | 2.0 | 8 | 1080 | 948 |
| April 30 | 2.0 | 8 | 2556 | 1440 | 2.0 | 8 | 624 | 348 |
| May 1 | 2.0 | 8 | 2784 | 1260 | 2.0 | 8 | 516 | 444 |
| May 2 | 2.0 | 8 | 516 | 720 | 1.5 | 6 | 0 | 0 |
| May 3 | 2.0 | 8 | 264 | 348 | 1.5 | 6 | 1416 | 1152 |
| May 4 | 2.0 | 8 | 1176 | 756 | 1.75 | 7 | 72 | 324 |
| May 5 | 2.0 | 8 | 9540 | 3120 | 1.5 | 6 | 2148 | 972 |
| May 6 | 2.0 | 8 | 1008 | 612 | 1.75 | 7 | 4848 | 2952 |
| May 7 | 2.0 | 8 | 144 | 84 | 2.0 | 8 | 1716 | 1056 |
| May 8 | 2.0 | 8 | 1812 | 1272 | 2.0 | 8 | 1692 | 744 |
| May 9 | 2.0 | 8 | 48 | 24 | 1.5 | 6 | 1068 | 492 |
| May 10 | 2.0 | 8 | -516 | 468 | 2.0 | 8 | 408 | 912 |
| May 11 | 2.0 | 8 | 0 | 84 | 1.5 | 6 | 1728 | 984 |
| May 12 | 2.0 | 8 | 7548 | 4776 | 2.0 | 8 | 300 | 228 |
| May 13 | 2.0 | 8 | 1980 | 1212 | 2.0 | 8 | 888 | 456 |
| May 14 | 2.0 | 8 | 204 | 300 | 1.75 | 7 | 336 | 204 |
| May 15 | 2.0 | 8 | 2652 | 1212 | 1.75 | 7 | -12 | 0 |
| May 16 | 2.0 | 8 | 264 | 156 | - | - | | |
| TOTALS | 45 | | 40584 | 23760 | 52.5 | | 113998 | 56340 |

Notes:

^a net movement = westward - eastward in spring
= eastward - westward in autumn

N₁, SE₁: 15 minute sample periods

N₂, SE₂: variable length sample periods used with ratio estimator (see Methods).

Appendix IB. Parameters of daily autumn migration watches during 1978, 1979, and 1980 on the eastern Copper River Delta, Alaska. See Appendix IA for notes.

| Date | 1978 | | | | 1979 | | | | | 1980 | | | | |
|---------|---------------|----------------|--------------------------------------|-----------------|---------------|----------------|----------------|--------------------------------------|-----------------|-----------------|---------------|----------------|--------------------------------------|-----------------|
| | Obs. Hours | N ₁ | Net ^a Birds /12hrs. | SE ₁ | Obs. Hours | N ₁ | N ₂ | Net ^a Birds /12hrs. | SE ₁ | SE ₂ | Obs. Hours | N ₂ | Net ^a Birds /12hrs. | SE ₂ |
| Aug 6 | | | | | 2.5 | 10 | 5 | 480 | 300 | 444 | | | | |
| Aug 7 | | | | | 2.3 | 9 | 5 | 108 | 96 | 96 | | | | |
| Aug 8 | | | | | 3.5 | 14 | 4 | 1260 | 636 | 396 | | | | |
| Aug 9 | .5 | 2 | 2904 | 2004 | 4.0 | 16 | 5 | 480 | 372 | 348 | | | | |
| Aug 10 | | | | | 5.2 | 21 | 3 | 804 | 264 | 504 | | | | |
| Aug 11 | 7 | 28 | 1220 | 288 | 6.0 | 25 | 4 | 816 | 204 | 156 | | | | |
| Aug 12 | 6.75 | 27 | 768 | 252 | 7.1 | 27 | 4 | 504 | 180 | 300 | | | | |
| Aug 13 | | | | | 7.4 | 28 | 5 | 468 | 528 | 420 | | | | |
| Aug 14 | 3.25 | 13 | -48 | 516 | 5.3 | 21 | 3 | 96 | 60 | 72 | | | | |
| Aug 15 | 1.0 | 4 | -48 | 36 | 5.7 | 20 | 5 | 156 | 252 | 300 | | | | |
| Aug 16 | | | | | 7.5 | 30 | 7 | -300 | 216 | 192 | | | | |
| Aug 17 | | | | | 5.9 | 24 | 5 | 828 | 264 | 252 | | | | |
| Aug 18 | | | | | 6.4 | 25 | 5 | 780 | 540 | 636 | | | | |
| Aug 19 | | | | | 6.3 | 25 | 3 | 564 | 180 | 84 | 3.2 | 4 | 588 | 576 |
| Aug 20 | 1.0 | 4 | 440 | 264 | | | | | | | 6.0 | 4 | -228 | 468 |
| Aug 21 | 2.75 | 11 | 228 | 228 | | | | | | | 1.2 | 1 | -1044 | 0 |
| Aug 22 | 2.0 | 8 | 804 | 432 | 1.0 | 4 | 1 | 1608 | 1596 | 0 | | | | |
| Aug 23 | 2.75 | 11 | 276 | 180 | 5.3 | 21 | 4 | 132 | 96 | 120 | 2.5 | 2 | -36 | 348 |
| Aug 24 | 3.0 | 12 | -420 | 936 | 3.5 | 15 | 5 | -96 | 264 | 192 | 4.3 | 3 | 156 | 60 |
| Aug 25 | 4.25 | 17 | 492 | 468 | 5.3 | 23 | 4 | 648 | 756 | 948 | 4.1 | 4 | 168 | 108 |
| Aug 26 | 4.0 | 16 | 2352 | 1332 | 7.0 | 28 | 5 | 324 | 228 | 264 | 3.8 | 3 | 60 | 408 |
| Aug 27 | 4.5 | 18 | 1584 | 552 | 4.3 | 17 | 5 | 0 | 84 | 96 | 4.3 | 4 | 552 | 552 |
| Aug 28 | 5.0 | 20 | 732 | 252 | 5.0 | 19 | 8 | 996 | 420 | 540 | 4.8 | 4 | 540 | 264 |
| Aug 29 | 3.75 | 15 | 156 | 1176 | 4.7 | 19 | 6 | 84 | 156 | 168 | 6.8 | 5 | 156 | 324 |
| Aug 30 | 2.75 | 11 | 36 | 84 | 6.8 | 27 | 5 | 420 | 264 | 264 | 4.8 | 3 | 288 | 132 |
| Aug 31 | 3.75 | 15 | 36 | 180 | 3.8 | 15 | 6 | 240 | 744 | 840 | 5.6 | 2 | 600 | 840 |
| Sept 1 | 1.75 | 7 | 312 | 288 | 5.5 | 23 | 3 | 1260 | 216 | 240 | 5.5 | 4 | 1176 | 732 |
| Sept 2 | 3.75 | 15 | 792 | 312 | 5.3 | 21 | 5 | 228 | 180 | 132 | 2.1 | 2 | 768 | 240 |
| Sept 3 | 3.75 | 15 | 720 | 180 | 3.8 | 15 | 5 | 768 | 252 | 276 | 1.0 | 2 | 660 | 636 |
| Sept 4 | 1.0 | 4 | 228 | 624 | 4.3 | 17 | 5 | 156 | 60 | 72 | | | | |
| Sept 5 | 3.25 | 13 | 12 | 120 | 3.7 | 15 | 5 | -36 | 132 | 144 | | | | |
| Sept 6 | 2.75 | 11 | 300 | 180 | 3.5 | 14 | 5 | 180 | 96 | 72 | | | | |
| Sept 7 | 3.75 | 15 | 336 | 348 | 6.4 | 25 | 8 | 84 | 60 | 60 | | | | |
| Sept 8 | 3.75 | 15 | -108 | 228 | 4.8 | 20 | 6 | 24 | 36 | 48 | | | | |
| Sept 9 | 3.75 | 15 | 96 | 96 | 3.8 | 15 | 5 | 108 | 48 | 48 | | | | |
| Sept 10 | 3.75 | 15 | -84 | 96 | 3.3 | 17 | 5 | 240 | 252 | 348 | | | | |
| Sept 11 | 2.25 | 9 | -12 | 48 | 2.8 | 11 | 5 | -156 | 156 | 192 | | | | |
| Sept 12 | | | | | 3.0 | 12 | 5 | -144 | 264 | 228 | | | | |
| Sept 13 | | | | | | | | | | | | | | |
| Sept 14 | | | | | 4.0 | 16 | 5 | -72 | 72 | 84 | | | | |

Appendix IB. (continued)
1978

| Date | 1978 | | | | 1979 | | | | | 1980 | | | | |
|---------|---------------|----------------|--------------------------------------|-----------------|---------------|----------------|----------------|--------------------------------------|-----------------|-----------------|---------------|----------------|--------------------------------------|-----------------|
| | Obs. Hours | N ₁ | Net ^a Birds /12hrs. | SE ₁ | Obs. Hours | N ₁ | N ₂ | Net ^a Birds /12hrs. | SE ₁ | SE ₂ | Obs. Hours | N ₂ | Net ^a Birds /12hrs. | SE ₂ |
| Sept 15 | | | | | 4.3 | 17 | 5 | -144 | 72 | 72 | | | | |
| Sept 16 | | | | | 4.0 | 17 | 6 | 252 | 108 | 132 | | | | |
| Sept 17 | | | | | 4.3 | 18 | 6 | -60 | 24 | 48 | | | | |
| Sept 18 | | | | | 5.1 | 20 | 6 | -60 | 72 | 48 | | | | |
| Sept 19 | 2.0 | 8 | 288 | 180 | 3.2 | 13 | 4 | -84 | 60 | 60 | | | | |
| Sept 20 | 1.75 | 7 | 180 | 132 | 2.5 | 10 | 4 | 36 | 24 | 36 | | | | |
| Sept 21 | 2.75 | 11 | 84 | 36 | 3.5 | 14 | 6 | -36 | 180 | 168 | | | | |
| Sept 22 | 2.5 | 10 | -96 | 288 | 1.3 | 4 | 1 | 156 | 84 | 0 | | | | |
| Sept 23 | 2.75 | 11 | 192 | 204 | 2.8 | 11 | 4 | 132 | 108 | 108 | | | | |
| Sept 24 | 3.5 | 14 | 120 | 204 | 3.6 | 14 | 7 | 24 | 192 | 192 | | | | |
| Sept 25 | 3.5 | 14 | 0 | 72 | 6.2 | 24 | 4 | 276 | 96 | 96 | | | | |
| Sept 26 | 3.0 | 12 | 108 | 60 | 3.0 | 12 | 3 | -72 | 36 | 24 | | | | |
| Sept 27 | 3.0 | 12 | 108 | 84 | 2.5 | 10 | 4 | -48 | 48 | 60 | | | | |
| Sept 28 | 2.75 | 11 | -108 | 132 | 4.6 | 18 | 4 | 12 | 36 | 36 | | | | |
| Sept 29 | .5 | 2 | -192 | 180 | 6.2 | 25 | 4 | 216 | 84 | 84 | | | | |
| Sept 30 | .75 | 3 | 156 | 144 | 1.0 | 4 | 3 | 24 | 12 | 24 | | | | |
| Oct 1 | 1.75 | 7 | 24 | 552 | 3.0 | 13 | 3 | 24 | 12 | 12 | | | | |
| Oct 2 | 2.5 | 10 | 420 | 312 | .8 | 3 | 2 | 144 | 72 | 0 | | | | |
| Oct 3 | 5.25 | 21 | 5712 | 2412 | 5.3 | 21 | 3 | 48 | 36 | 24 | | | | |
| Oct 4 | 2.0 | 8 | -420 | 528 | 1.0 | 4 | 1 | 0 | 0 | 0 | | | | |
| Oct 5 | 2.5 | 10 | -264 | 132 | 1.0 | 4 | 2 | 0 | 0 | 0 | | | | |
| Oct 6 | 1.0 | 4 | 108 | 96 | 2.3 | 10 | 4 | 60 | 444 | 384 | | | | |
| Oct 7 | 1.0 | 4 | 0 | 0 | 4.8 | 19 | 4 | -120 | 228 | 252 | | | | |
| Oct 8 | - | | | | | | | | | | | | | |
| Oct 9 | 2.25 | 9 | -828 | 2880 | 3.5 | 14 | 4 | 60 | 24 | 48 | | | | |
| Oct 10 | 3.0 | 12 | 4512 | 2340 | 3.9 | 15 | 3 | 96 | 60 | 84 | | | | |
| Oct 11 | 3.0 | 12 | 4248 | 1944 | 4.1 | 15 | 3 | 672 | 408 | 240 | | | | |
| Oct 12 | 1.5 | 6 | 1128 | 876 | 1.0 | 4 | 2 | 288 | 276 | 144 | | | | |
| Oct 13 | 2.5 | 10 | 8136 | 2160 | 8.7 | 34 | 1 | 4836 | 576 | 0 | | | | |
| Oct 14 | 3.0 | 12 | 2820 | 828 | 4.8 | 19 | 4 | 1104 | 480 | 84 | | | | |
| Oct 15 | 2.5 | 10 | -48 | 216 | 4.3 | 15 | 3 | 0 | 0 | 0 | | | | |
| Oct 16 | .25 | 1 | 0 | 0 | 3.0 | 12 | 3 | -108 | 96 | 96 | | | | |
| Oct 17 | | | | | 4.2 | 17 | 3 | 12 | 36 | 96 | | | | |
| Oct 18 | | | | | 3.0 | 12 | 3 | 1584 | 576 | 864 | | | | |
| Oct 19 | | | | | 1.8 | 8 | 2 | 0 | 0 | 0 | | | | |
| Oct 20 | | | | | 2.4 | 11 | 3 | -240 | 144 | 96 | | | | |
| Oct 21 | | | | | 2.5 | 11 | 3 | 348 | 612 | 612 | | | | |
| TOTALS | 154.25 | | 40492 | 28752 | 299.5 | | | 23472 | 15852 | 13800 | 63 | | 4404 | 5688 |

Appendix II. Descriptions of habitats classified on the eastern Copper River Delta, Alaska. Classifications according to Cowardin et al. (1979) are given in parentheses for each vegetated wetland type.

I. WETLANDS

1. Intertidal Mud and Sand. This habitat is extensive ECRD, but is completely unvegetated and therefore of little interest except as future vegetated wetland, which will develop as siltation continues in the lagoon system.

2. Saltmarsh. (SYSTEM estuarine, SUBSYSTEM intertidal, CLASS emergent, SUBCLASS non-persistent, WATER REGIME irregularly flooded, WATER CHEMISTRY mixohaline): This habitat is entirely flooded by brackish water at least once per year, the lower portions much more frequently. There are no ponds except on Strawberry Reef. Vegetation cover is generally sparse (<50%), and shrubs only present in small numbers at the interface with the adjacent Freshwater Meadow. Most plants are less than 20 cm tall, and visibility is thus virtually unlimited at a height of 30 or 40 cm. As is the case with the Freshwater Meadow (see below), the vegetation of the Saltmarsh is changing rapidly, and thus does not nicely segregate into any of the saltmarsh communities previously described from southcentral Alaska (summarized in Batten [1980]). A variety of communities are found, depending on microhabitat differences, between Softuk Lagoon and Cottonwood Point, and additional ones on Strawberry Reef. Batten et al. (1978) have described the vegetation of Softuk Lagoon in more

detail.

Generally, across the mainland of the ECRD, the most seaward vegetation is composed of Puccinellia nutkaensis, with lesser amounts of Carex lyngbyaei, Carex ramenskii, Triglochin maritimum, T. palustris, and Eleocharis palustris. Slightly further inland the dominants are still Puccinellia nutkaensis, and Carex lyngbyaei, but Plantago maritima, and especially Potentilla egedii also become important. In the uppermost, least frequently flooded zone, C. lyngbyaei remains dominant, with lesser amounts of Deschampsia caespitosa, Juncus arcticus, Puccinellia nutkaensis, Potentilla egedii, and T. maritimum.

The Saltmarsh on the landward side of Strawberry Reef has developed a unique community compared to the rest of the ECRD. Eleocharis acicularis is the dominant in the lowest zone, while further up there is an almost pure stand of Carex lyngbyaei. Triglochin palustris, a fairly common, but inconspicuous plant of the Saltmarsh elsewhere on the ECRD, is abundant in patches in the upper edge of the Eleocharis zone. There are several very productive brackish ponds.

An extensive area of pioneering vegetation lying west of Cottonwood Dunes and dissected by braided channels of the Copper and Martin Rivers is not clearly influenced by tidal action, yet at first glance resembles the Saltmarsh. Most likely it was flooded by the essentially fresh waters of the Copper River prior the earthquake, and is now undergoing primary succession without any flooding

influences. It contains several stands of pure Carex lyngbyaei, and an "island" containing willows up to 1.5 m tall, located about 2 km NW of Cottonwood Point. Otherwise, the majority of the area is covered with very sparse growth of Eleocharis palustris and Equisetum arvense. The substrate is sandy, but saturated almost to the surface, and feels very unstable underfoot.

3. Freshwater Meadow. (SYSTEM palustrine, SUBSYSTEM none, CLASS emergent wetland, shrub scrub wetland, SUBCLASS persistent, WATER REGIME saturated or temporarily flooded, WATER CHEMISTRY fresh): This is a complex type, actually composed of many communities growing in a fine-grained mosaic. It contains an extensive dendritic network of previously tidal drainage channels, all but the largest of which are now above tidal influence and partially or wholly colonized with vegetation. The major plant communities are dominated by one of the following: grasses (Calamagrostis canadensis, Poa eminens, Deschampsia caespitosa, Agrostis alaskana, Eriophorum russeolum); sedges (usually Carex lyngbyaei, C. ramenskii, Juncus arcticus, Juncus alpinus); shrubs of all sizes up to and some exceeding 4 m in height (Alnus sinuata, Salix spp., Myrica gale, and Picea sitchensis); and mosses. Horsetail (Equisetum arvense), and a wide variety of forbs (most commonly Potentilla egedii, Epilobium spp., Rhinanthus minor, Parnassia palustris, Chrysanthemum arcticum, Lupinus nootkatensis, and Cicuta spp.) occur in these subunits. Complete plant lists are presented in Appendices III, IV, and V.

Shrub invasion, particularly by alders, is most pronounced on levees and along the coastal fringe of this habitat, and least pronounced in the wetter semi-developed basins. Although the substrate is usually saturated in most areas, standing water is not conspicuous, except after periods of particularly heavy rain such as are common in the autumn. Where such shallow standing water is found semi-permanently, emergent aquatics such as Eleocharis palustris, Hippurus vulgaris, Potentilla palustris, and Equisetum fluviatile are found. The few permanent ponds are confined to the western and northeastern peripheries of the Freshwater Meadow where sedge basins are well-developed, and the northern perimeter, where beaver dams, floating mat shorelines, extensively shrubbed levees, and other features begin to appear which are characteristic of the next zone inland (Shrub Marsh).

The vegetation of the Freshwater Meadow is in a state of rapid succession owing to the uplift associated with the 1964 earthquake. This undoubtedly accounts for the diversity and interspersed of plant species and plant communities, and the lack of strict conformity with the communities of other coastal wetlands in Alaska (see Batten 1980).

4. Shrub Marsh. (SYSTEM palustrine, SUBSYSTEM none, CLASS emergent wetland, shrub scrub wetland, aquatic bed, SUBCLASS persistent, WATER REGIME saturated to permanently flooded, WATER CHEMISTRY fresh): This habitat lies inland from the Freshwater Meadow and is characterized

by a deep organic layer and floating mats in many of the open meadows. Drainage is extremely poor and there are numerous lakes and ponds with poorly defined shorelines and extensive emergent vegetation. Most of the poor drainage is attributable to beaver dams. Shrubs, primarily alder, and trees (Populus trichocarpa and Picea sitchensis) occupy levees and other high ground. Alnus, Salix spp. and Myrica gale are abundant throughout.

I did no groundwork in this habitat, but Sheierl and Meyer (1977) described it in some detail, and Hansen et al. (1971) described similar habitat used by breeding trumpeter swans (Olor buccinator) in the Martin River and Bremner River areas.

II. UPLANDS

The following are described only briefly because they are not of primary importance in the present study.

5. Coniferous Upland. Closed forests of Sitka spruce cover the lower slopes of the Ragged Mountains to the east of the ECRD, as well as several "islands" of upland formed by rock outcrops jutting through the sediments of the ECRD. Bog meadows are interspersed with the coniferous forest on the more gently rolling hills east of Softuk Lagoon and between Softuk Lagoon and Mirror Slough.

6. Deciduous Upland. Closed canopies of tall shrubs, primarily alder, with some willow and cottonwood, are found on the wind-formed dunes

adjacent to the Copper River.

7. Elymus Dune. This type is dominated by beach rye grass (Elymus arenarius), and is found on an extensive area of Strawberry Reef and a smaller portion of Softuk Spit. A few small thickets of spruce, alder, and willow occur within this zone on Strawberry Reef.

Appendix III. Cover and frequency of occurrence of plants found on 129 1-m² vegetation plots in Freshwater Meadow habitat on the eastern Copper River Delta, Alaska, during July and August 1979.

| | Mean percent cover | Percent frequency of occurrence |
|---|--------------------|---------------------------------|
| <i>Aulacomnium palustre</i> | 17.7 | 50.4 |
| <i>Drepanocladus uncinatus</i> | 11.5 | 34.9 |
| <i>Rhytidiadelphus squarrosus</i> | 10.7 | 27.9 |
| <i>Mnium pseudopunctatum</i> | 8.0 | 45.7 |
| <i>Helodium blandowii</i> | 5.4 | 33.3 |
| <i>Psilopilum laevigatum</i> and <i>Dicranella</i> sp. | 5.2 | 12.4 |
| <i>Polytrichum commune</i> | 4.4 | 25.6 |
| <i>Myrica gale</i> | 4.2 | 24.8 |
| <i>Carex lyngbyaei</i> | 3.8 | 51.2 |
| <i>Alnus sinuata</i> | 3.4 | 31.0 |
| ^a Upright <i>Salix</i> spp. | 3.3 | 32.5 |
| <i>Potentilla egedii</i> | 2.6 | 75.2 |
| <i>Equisetum arvense</i> and <i>Equisetum fluviatile</i> | 1.9 | 55.0 |
| ^b Dwarf <i>Salix</i> spp. | 1.8 | 33.3 |
| <i>Agrostis alaskana</i> and <i>Agrostis geminata</i> | 1.0 | 44.2 |
| <i>Poa eminens</i> | 0.86 | 48.8 |
| <i>Juncus alpinus</i> | 0.81 | 27.9 |
| <i>Sphagnum squarrosum</i> | 0.70 | 8.5 |
| <i>Epilobium palustre</i> and <i>Epilobium hornemannii</i> | 0.53 | 63.6 |
| <i>Parnassia palustris</i> | 0.51 | 50.4 |
| <i>Potentilla palustris</i> | 0.46 | 10.1 |
| <i>Deschampsia caespitosa</i> | 0.46 | 22.5 |
| <i>Epilobium angustifolium</i> | 0.45 | 3.1 |
| <i>Chrysanthemum arcticum</i> | 0.44 | 26.4 |
| <i>Eleocharis kamschatica</i> | 0.43 | 12.4 |
| <i>Calamagrostis deschampsoides</i> | 0.41 | 21.7 |
| <i>Calamagrostis canadensis</i> | 0.41 | 32.6 |
| <i>Peltigera</i> sp. | 0.35 | 17.8 |
| <i>Primula egaliksensis</i> | 0.30 | 9.3 |
| <i>Rhinanthus minor</i> | 0.29 | 46.5 |
| <i>Populus trichocarpa</i> | 0.28 | 3.9 |
| <i>Picea sitchensis</i> | 0.21 | 6.2 |
| <i>Triglochin maritimum</i> | 0.21 | 17.1 |
| <i>Galium trifidum</i> | 0.21 | 29.5 |
| ^c <i>Stellaria</i> spp. | 0.20 | 32.5 |
| <i>Lathyrus palustris</i> | 0.19 | 5.4 |

Appendix III. (cont.)

| | Mean percent cover | percent frequency of occurrence |
|---|--------------------|---------------------------------|
| <i>Carex mackenziei</i> | 0.19 | 5.4 |
| <i>Carex pluriflora</i> | 0.19 | 2.3 |
| <i>Eriophorum scheuchzeri</i> | 0.18 | 16.3 |
| <i>Rumex fenestratus</i> | 0.17 | 8.5 |
| <i>Pyrola asarifolia</i> | 0.15 | 1.5 |
| <i>Spiranthes romanzoffiana</i> | 0.14 | 22.5 |
| <i>Hedysarum alpinum</i> | 0.12 | 1.6 |
| <i>Carex aquatilis</i> | 0.12 | 4.6 |
| <i>Ranunculus cymbalaria</i> | 0.11 | 13.9 |
| <i>Epilobium adenocaulon</i> | 0.10 | 10.9 |
| <i>Agrostis exarata</i> | 0.08 | 7.0 |
| <i>Plantago maritima</i> | 0.08 | 5.4 |
| <i>Viola epipsila</i> | 0.08 | 3.8 |
| <i>Lycopodium</i> sp. | 0.08 | 1.5 |
| <i>Hippuris tetraphylla</i> | 0.07 | 2.3 |
| <i>Cicuta douglasii</i> and <i>Cicuta mackenzieana</i> | 0.06 | 5.4 |
| <i>Euphrasia mollis</i> | 0.06 | 10.8 |
| <i>Drosera rotundifolia</i> | 0.05 | 1.6 |
| Mushroom spp. | 0.04 | 7.0 |
| <i>Triglochin palustris</i> | 0.04 | 7.8 |
| <i>Lomatogonium rotatum</i> | 0.03 | 6.2 |
| <i>Pedicularis verticillata</i> | 0.03 | 2.3 |
| <i>Juncus arcticus</i> | 0.02 | 3.1 |
| <i>Juncus castaneus</i> | 0.02 | 1.5 |
| <i>Festuca rubra</i> | 0.02 | 5.4 |
| <i>Festuca altaica</i> | 0.02 | 3.1 |
| <i>Eriophorum russeolum</i> | 0.01 | 1.5 |
| <i>Carex kelloggii</i> | 0.01 | 0.8 |
| <i>Carex laeviculmis</i> | 0.01 | 2.3 |
| <i>Hierochloa odorata</i> | 0.01 | 2.3 |
| <i>Iris setosa</i> | 0.01 | 0.8 |
| <i>Juncus falcata</i> | 0.01 | 0.0 |
| <i>Menyanthes trifoliata</i> | 0.01 | 0.8 |
| <i>Platanthera dilatata</i> | 0.01 | 0.8 |
| <i>Ranunculus hyperboreus</i> | 0.01 | 0.8 |
| <i>Athyrium felix-femina</i> | 0.01 | 0.8 |
| <i>Hammarbya paludosa</i> | 0.01 | 0.8 |

^a Willows of upright growth form, including: *Salix alaxensis*, *S. barclayi*, *S. commutata*, *S. scouleriana*, and *S. sitchensis*.

^b Willows of mat-forming growth form, including: *S. arctica* and *S. ovalifolia*.

^c Including: *S. calycantha*, *S. humifusa*, and *S. longifolia*.

Appendix IV. Cover and frequency of occurrence of plants found on 24 1-m² vegetation plots in Saltmarsh habitat on the eastern Copper River Delta, Alaska, during July and August 1979.

| | Mean percent cover | Percent frequency of occurrence |
|----------------------------------|--------------------|---------------------------------|
| <i>Psilopilum laevigatum</i> and | | |
| <i>Dicranella</i> sp. | 39.6 | 20.8 |
| <i>Carex ramenskii</i> | 18.2 | 16.7 |
| <i>Plantago maritima</i> | 11.7 | 50.0 |
| <i>Potentilla egedii</i> | 8.6 | 54.2 |
| <i>Puccinellia</i> spp. | 4.2 | 75.0 |
| <i>Deschampsia caespitosa</i> | 3.9 | 37.5 |
| <i>Carex lyngbyaei</i> | 2.7 | 20.8 |
| <i>Equisetum arvense</i> | 1.5 | 16.7 |
| <i>Juncus arcticus</i> | 1.5 | 37.5 |
| <i>Myrica gale</i> | 1.4 | 4.2 |
| <i>Alnus sinuata</i> | 1.3 | 4.2 |
| <i>Juncus bufonius</i> | 1.0 | 8.3 |
| Dwarf <i>Salix</i> spp. | 0.8 | 8.3 |
| <i>Ranunculus cymbalaria</i> | 0.7 | 16.7 |
| <i>Triglochin palustris</i> | 0.7 | 8.3 |
| <i>Parnassia palustris</i> | 0.4 | 16.7 |
| <i>Epilobium palustre</i> | 0.3 | 12.5 |
| <i>Epilobium angustifolium</i> | 0.3 | 4.2 |
| <i>Hordeum brachyantherum</i> | 0.2 | 8.3 |
| <i>Juncus alpinus</i> | 0.2 | 12.5 |
| <i>Chrysanthemum arcticum</i> | 0.2 | 4.2 |
| <i>Rhinanthus minor</i> | 0.2 | 8.3 |
| <i>Polygonum fowleri</i> | 0.2 | 4.2 |
| <i>Polytrichum commune</i> | 0.1 | 4.2 |
| <i>Agrostis exarata</i> | 0.1 | 4.2 |
| <i>Agrostis alaskana</i> and | | |
| <i>Agrostis geminata</i> | 0.2 | 4.2 |

Appendix V. Plants identified on the eastern Copper River Delta, Alaska, but not found on systematic vegetation plots in Freshwater Meadow or Saltmarsh habitats. Species occurring only on gravel bars along major sloughs or on sand dunes (a), in acidic bog (b), or in Coniferous Uplands (c) are noted.

| | |
|---|---|
| <i>Achillea borealis</i> | <i>Myriophyllum spicatum</i> |
| <i>Alopecurus aequalis</i> | ^b <i>Nuphar polysepalum</i> |
| ^b <i>Andromeda polifolia</i> | <i>Oxycoccus microcarpus</i> |
| ^c <i>Aquilegia formosa</i> | <i>Phyllodoce aleutica</i> |
| <i>Arctophila fulva</i> | <i>Pinguicula vulgaris</i> |
| <i>Aruncus sylvestris</i> | <i>Polemonium acutiflorum</i> |
| ^c <i>Boschniakia rossica</i> | ^a <i>Polygonum viviparum</i> |
| ^c <i>Botrychium lunaria</i> | <i>Potentilla villosa</i> |
| <i>Callitriche verna</i> | <i>Potamogeton natans</i> |
| <i>Caltha palustris</i> | <i>Potamogeton pectinatus</i> |
| <i>Cardamine pratensis</i> | <i>Potamogeton perfoliatus</i> |
| <i>Carex rhyncophysa</i> | <i>Prenanthes alata</i> |
| <i>Carex rostrata</i> | <i>Rhododendron camtschaticum</i> |
| <i>Carex sitchensis</i> | ^c <i>Ribes laxiflorum</i> |
| <i>Cassiope stellariana</i> | ^a <i>Rorrippa islandica</i> |
| <i>Castilleja chrymactis</i> | ^c <i>Rubus pedatus</i> |
| <i>Corallorrhiza trifida</i> | <i>Rubus spectabilis</i> |
| <i>Cornus canadensis</i> | <i>Sagina intermedia</i> |
| ^b <i>Dodecatheon jeffreyi</i> | ^c <i>Sambucus callicarpa</i> |
| ^c <i>Dryopteris dilatata</i> | <i>Sanguisorba stipulata</i> |
| ^c <i>Echinopanax horridum</i> | <i>Saxifraga punctata</i> |
| <i>Eleocharis acicularis</i> | <i>Scirpus validus</i> |
| <i>Elymus arenarius</i> | <i>Sedum rosea</i> |
| <i>Empetrum nigrum</i> | ^a <i>Senecio pseudo-arnica</i> |
| ^a <i>Epilobium latifolia</i> | <i>Solidago lepida</i> |
| <i>Eriophorum angustifolium</i> | <i>Sparanium angustifolium</i> |
| <i>Fritillaria camtschaticensis</i> | <i>Spiraea beauverdiana</i> |
| ^b <i>Gentiana douglasiana</i> | <i>Streptopus amplexifolius</i> |
| ^c <i>Geranium erianthum</i> | ^c <i>Tiarella trifoliata</i> |
| <i>Geum calthifolia</i> | <i>Trientalis europaea</i> |
| ^a <i>Geum macrophyllum</i> | ^c <i>Tsuga heterophylla</i> |
| ^a <i>Glehnia littoralis</i> | ^c <i>Vaccinium ovalifolium</i> |
| ^c <i>Gymnocarpium dryopteris</i> | <i>Vaccinium uliginosum</i> |
| <i>Heuchera glabra</i> | ^c <i>Veratrum viride</i> |
| <i>Hippuris vulgaris</i> | ^c <i>Viburnum edule</i> |
| ^a <i>Honckenya peploides</i> | |
| <i>Isoetes truncata</i> | |
| ^c <i>Lysichiton americanum</i> | |
| ^c <i>Maianthemum dilatatum</i> | |
| <i>Malaxis monophylla</i> | |
| ^c <i>Menziesia ferruginea</i> | |
| ^c <i>Mimulus guttatus</i> | |
| <i>Moehringia laterifolia</i> | |
| ^c <i>Moneses uniflora</i> | |