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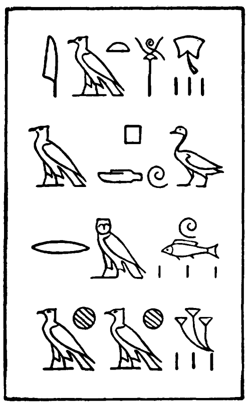

THE TRUMPETER SWAN IN ALASKA

by

HENRY A. HANSEN, PETER E. K. SHEPHERD,
JAMES G. KING, AND WILLARD A. TROYER

OCTOBER 1971 NO. 26

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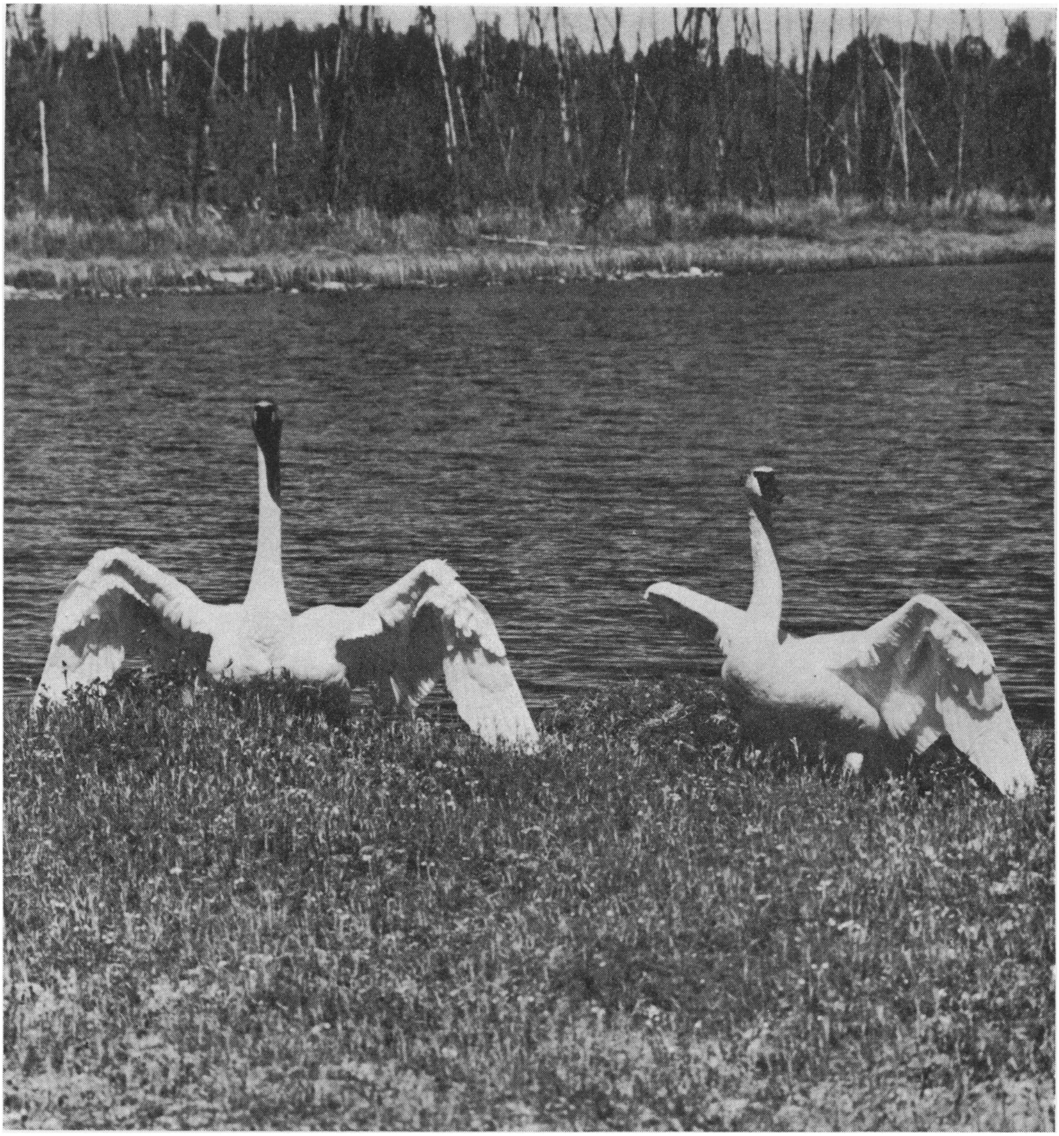

FRONTISPIECE. A pair of trumpeter swans on the Kenai National Moose Range defending their nest against an intruding floatplane from which the picture was taken. (Photo by Troyer)

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THE TRUMPETER SWAN IN ALASKA

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CONTENTS

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INTRODUCTION

To paraphrase naturalist–philosopher Aldo Leopold, the real superiority of man over beast lies in the fact that man has the capacity to mourn the death, or well-being, of another species. Superiority of this stripe implies a concomitant moral responsibility for stewardship summarized by an ancient Persian proverb: God will not seek thy race, nor will He ask thy birth: alone, He will demand of thee, "What hast thou done on earth?"

Too often in recent history man has induced a spate of mourning by accelerating the demise of another species. It is gratifying, therefore, to witness the turn of the tide with the first species brought back from the brink in America through a conscious, concerted effort.

Long regarded as nearly extinct, the trumpeter swan (*Olor buccinator* Richardson) has recovered sufficiently south of Canada that it was officially declared, in December 1968, to be no longer an endangered species even though the population is still numerically weak by many standards. This remarkable recovery is, in part, the result of protection from legalized hunting, management of remnant populations, and the beginning of a successful transplanting program from the Red Rock Lakes National Wildlife Refuge to other areas within the trumpete swan's ancestral breeding range. In all, it is symbolic of the purpose and fulfillment of good stewardship and illustrates what can be accomplished through combined and integrated effort.

At a time when trumpeter swans may have been at the lowest population level in the history of their species, Bent (1925) lamented that "This magnificent bird, the largest of all North American wildfowl, belongs to a vanishing race . . . ." He could now take comfort in the knowledge that his prophecy, clear though it may have seemed at the time, was premature and, hopefully, need not recur.

Recent discoveries of substantial breeding and wintering populations of trumpeter swans in Alaska and along the North Pacific coast were instrumental in prompting a broad-scale study designed to provide both ecological data and to determine population status. Little was known concerning the environmental requirements of these trumpeter swans, their migration patterns, breeding biology, numerical status, and tolerance to disturbance factors.

With rapid human population growth and industrial development imminent in Alaska, drastic changes in habitat probably will occur. New road systems will be built, opening hitherto inaccessible areas to mining, logging, industrial, and recreational interests. Widespread oil discoveries and highly mineralized areas offer enticing rewards to venturesome industrialists. A vast hydroelectric potential exists in Alaska. Much of the development will occur within the range of the trumpeter swan and, if a healthy population is to be maintained, we must have a better understanding of its requirements. We must analyze, both quantitatively and qualitatively, the existing plant communities which constitute swan breeding and wintering habitat, as well as determine the ecological and human tolerances of this species and to what extent it will adapt if gross floral and faunal changes occur in its present environment. Until this analysis is accomplished, it is not possible to know what action, if any, will be needed to guarantee the trumpeter swan a place in which to live.

Spurred by Santayana's (1905) admonition that "Those who cannot remember the past are condemned to repeat it," we initiated a research study with the following objectives:

(1) determine the extent of the breeding range of the trumpeter swan in Alaska;
(2) ascertain the approximate breeding population;
(3) determine the migratory route and wintering grounds of this swan population;
(4) study possible adverse habitat alter-

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ation or disturbance through industrial development, e.g., dams, roads, mining, oil development, and lumbering;

(5) conduct a detailed ecological study of the swan breeding grounds on the lower Copper River system; and

(6) study the breeding biology of the trumpeter swan initially in the lower Copper River Basin and later on the Kenai National Moose Range as well.

The study was started during the summer of 1957 and conducted with a varying degree of intensity through 1968. Each of us contributed to the overall study at various times and in various capacities. Fluctuations in funding and conflicting responsibilities disrupted the smooth continuity of the project over its 12-year span. Nevertheless, a reasonably good picture of the trumpeter swan in Alaska has emerged.

Shepherd conducted an intensive ecological study of the trumpeter swan and its habitat on the lower Copper River system from June 1957 through August 1959 in partial fulfillment of the requirements for a Master of Science Degree at Washington State University. Hansen assisted as field supervisor of the project in conjunction with his overall responsibility for waterfowl research in Alaska from 1955 through 1964 and prepared the manuscript for this monograph. King provided much of the flying during the early years of the project and organized the extensive survey in 1968 to determine the current status of trumpeter swans throughout their range in Alaska. In 1964, Troyer expanded earlier studies on the Kenai National Moose Range into a detailed study of territoriality, molting, preflight brood movements, and other behavioral characteristics of that segment of the trumpeter swan population which is a good supplement to Shepherd's earlier work on the Copper River drainage.

In retrospect we realize that this study, in some respects, has done little more than reveal a wide array of unanswered or partially answered questions. In other respects we hope that we may have brushed the foundation strokes on a sturdy canvas and left behind a sketch from which our successors can paint a fuller and brighter future for the trumpeter swan. To attack the unsatisfied questions a whole host of potential projects present themselves. All of them would contribute to a better understanding of the trumpeter swan's life style and its perpetuation as a species. They all interrelate within a coordinated study that includes (1) an adequate delineation of winter range and abundance of trumpeters on the wintering grounds, (2) place and cause of mortality after 6 months of age, (3) banding, color marking, and telemetry, (4) the relationship of spring break-up to acquisition of territory, breeding behavior, and nidification, and (5) frequent enough and complete censuses on the breeding grounds to determine accurately the trumpeter swan's extension of range and population growth.

ACKNOWLEDGMENTS

We gratefully acknowledge the cheerful assistance of an array of employees from the Alaska Department of Fish and Game, the University of Alaska, and the Bureau of Sport Fisheries and Wildlife throughout the many years this study was in progress. In the early stages, during Shepherd's intensive research, Drs. George E. Hudson, Irvin O. Buss, Rexford F. Daubenmire, Richard A. Parker, and Charles W. McNeil, all of Washington State University, were particularly helpful and encouraging. Notable among the field assistants during this period was Lloyd Davis, an Eskimo from Selawik, whose lack of formal training did not detract from his keen observations and accurate records. He was also a good campfire companion.

David Spencer, John Hakala, Averill Thayer, Robert Richey, James Bartonek, and Bob Burkholder of the Bureau of Sport Fisheries and Wildlife, Sigurd Olson of the U.S. Forest Service, and Jim Branson of

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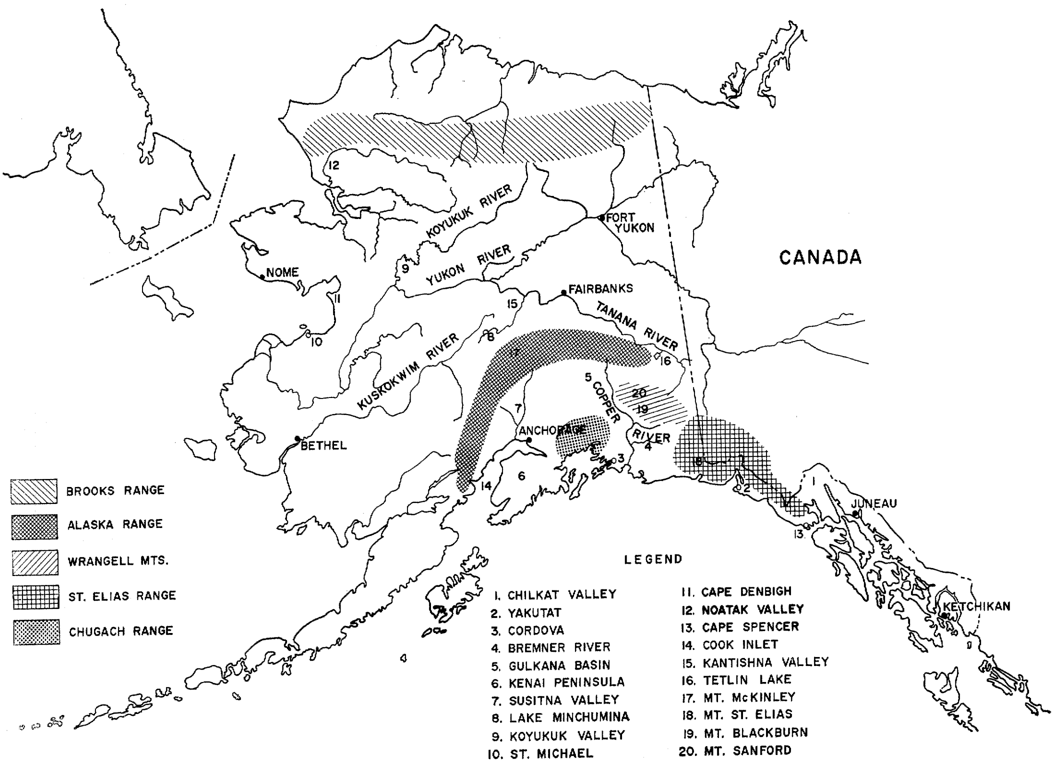

FIG. 1. Map of Alaska showing location of major place names mentioned in text.

the Bureau of Commercial Fisheries all participated at various times in the aerial surveys, frequently requiring an adjustment in their otherwise busy schedules. Loyal Johnson of the Alaska Department of Fish and Game unselfishly provided us with population data from his 1968 studies in the Cordova area. Dr. Calvin J. Lensink of the Bureau of Sport Fisheries and Wildlife provided an intangible, yet invaluable, service through long discussions helping to interpret and understand our findings. Photo credits are shown in each instance.

Special thanks goes to Jill Shepherd who contributed countless, patient hours of clerical work in the early stages of the manuscript and to Doris Hansen, Rosetta Johnson, and Patricia Wisniewski who performed a similar service in the later stages. Without understanding wives and secretaries science manuscripts could easily atrophy during gestation.

SURVEY AREA

General Description

That part of Alaska in which the trumpeter swan aerial studies were conducted extends along the Pacific coast from Cape Spencer on the east to Cook Inlet on the west and inland across the summit of the Alaska Range to include the Tanana and Kantishna river valleys. The topography of the area is rugged, with nearly all the highest peaks in Alaska occurring within or adjacent to its boundaries. Among these are Mt. McKinley (20,300 ft), Mt. St. Elias (18,008 ft), Mt. Blackburn (16,523), Mt. Sanford (16,208), and many peaks from 10,000 to 12,000 ft high (Fig. 1).

Glaciers and ice caps, remnants of the last great ice age, are numerous in these mountains. Traces of former glaciation are evident in the "U"-shaped and "hanging"

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TABLE 1.—COMPARATIVE WEATHER DATA FOR TRUMPETER SWAN BREEDING AREAS (LONG-TERM AVERAGES FROM U. S. WEATHER BUREAU)

	Apr	May	Jun	Jul	Aug	Sep	Oct	Average Summer May to Aug	Average Annual
					Average Precipitation				
Gulf Coast									
Cordova	5.07	6.44	4.19	6.44	9.72	15.47	15.56	26.79	98.64
Yakutat	7.98	7.92	4.96	8.63	10.54	16.32	19.93	32.05	139.15
Gulkana	.26	.66	1.38	2.15	2.45	2.06	1.37	6.64	14.70
Fairbanks	.29	.74	1.37	1.92	2.26	1.21	.92	6.29	11.92
Cook Inlet									
Talkeetna	.82	1.39	1.89	3.04	5.54	4.42	3.01	11.85	28.85
Anchorage	.40	.51	.89	1.55	2.56	2.71	1.87	6.29	14.27
					Average Temperature				
Gulf Coast									
Cordova	36.4	42.9	49.3	53.3	53.4	48.0	40.8	48.5	38.6
Yakutat	36.5	43.3	49.5	52.7	52.8	48.4	41.7	49.6	39.3
Gulkana	29.6	42.2	51.8	55.2	51.7	43.3	29.9	50.2	28.3
Fairbanks	28.9	47.4	59.3	60.9	55.6	44.6	27.5	55.8	26.2
Cook Inlet									
Talkeetna	33.7	44.4	54.8	58.0	54.5	46.2	33.6	52.9	35.3
Anchorage	35.4	45.7	53.7	57.3	55.6	48.0	36.0	53.1	33.2

valleys, cirques, and moraines. These glacial fields and high mountains, with relatively steep slopes extending to the ocean, influence the climate with the nearby north Pacific Ocean exerting a modifying effect on daily and seasonal temperature and precipitation ranges near the coast. The proximity of the precipitous Chugach Mountains to the moisture-saturated air from the Gulf of Alaska results in an annual precipitation of some 100 inches along the coast with a mean annual temperature of 38 to 39 F. Conversely, Gulkana, which is in the rain shadow of the Chugach Range 120 air miles north of Cordova, exhibits a continental climate with average annual precipitation of less than 15 inches and a mean annual temperature of 28 F. Farther inland, north of the Alaska Range in the Tanana Valley, the average annual precipitation is less than 12 inches with a mean annual temperature of approximately 26 F (Table 1). However, the most important climatological data in relation to the ecology of the trumpeter swans throughout their range in Alaska are not the annual or monthly medians, but the temperatures preceding the nesting period and the fall migration which cause ice destruction in the spring and ice formation in the fall. This is discussed in detail in the chapter on distribution and population status.

Altitude appeared to have little bearing on trumpeter swan distribution except as it influenced the availability of habitat. Nesting swans were sighted from sea level to a maximum altitude of 2,700 ft (Table 2). Otherwise suitable habitat above this elevation is precluded from use by the swans because of an inadequate ice-free period during the abbreviated summer.

Differences in terrestrial vegetation between coastal and inland areas are in part a reflection of the differences in rainfall

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TABLE 2.—ALTITUDE IN FEET ABOVE MEAN SEA LEVEL OF TRUMPETER SWAN SIGHTINGS, 1968

	Highest	Lowest	Normal
Gulf Coast	300	10	Under 100
Copper Canyon	400	200	Under 300
Gulkana Basin	2,709	1,600	2000–2500
Fairbanks	700	300	300–400
Cook Inlet	1,122	40	Under 300
Kenai	1,255	40	Under 300

and temperature. Characteristic forest species of both the coastal and interior climates are evident in south-central Alaska, often with broad intergradation of both types near the coast. The vegetation of the coastal areas of south-central Alaska is essentially an extension of the southeastern Alaska forests. This vegetation is dominated by (1) western hemlock (*Tsuga heterophylla*); (2) mountain hemlock (*Tsuga mertensiana*); and (3) Sitka spruce (*Picea sitchensis*). Wide variation exists in the distribution and abundance of these species, with western hemlock forming nearly pure stands to the east and becoming less common to the west. Mountain hemlock is common around Prince William Sound and on the east side of the Kenai Peninsula. Sitka spruce occurs nearly everywhere, but constitutes little of the actual forest cover. Infrequently, one may find stands of Alaska cedar (*Chamaecyparis nootkatensis*), but the species is of little importance ecologically.

Intensive Study Areas

Bremner River

The Bremner River enters the larger Copper River from the east, 40 miles from the mouth of the Copper River at 144°45′ west longitude and 61°00′ north latitude. The land relief of this area, in the rugged Chugach Range, varies greatly, from 8,530 ft (Hanagita Peak) to 200 ft near the confluence of the 2 rivers, with an average elevation of 6,000 to 7,000 ft.

Glacial ice once covered this region to a depth of 5,000 ft. Two groups of sedimentary rocks occupy most of the Bremner district. An older rock layer is formed of schists, slates, and limestone. A mesozoic bed, composed of interstratified slate and graywacke, is folded and faulted, but less metamorphosed than other beds to the north (Moffit 1914). Much of this rock has been eroded by water into steep canyons on the upper Bremner River.

The Bremner River drains an area of 1,000 square miles south of the Wrangell Mountains. A few large glaciers supply most of the Bremner River water which fluctuates considerably both seasonally and daily. The differences appear to be regulated to some extent by annual snowfall but largely by the rate at which the glacial ice melts. Warm, clear summer weather serves to maintain a steady ice melt, with diurnal fluctuations of 6 to 8 inches. Cloudy, cool summer weather results in a steady decrease in water after the spring runoff, accompanied by little diurnal fluctuation. The latter conditions were prevalent during 1958 and 1959 when the river levels dropped nearly 6 ft from June to August.

Numerous ponds in the lower Bremner River Valley are a result of imperfect drainage, river action, and beaver activity (Fig. 2). In addition, there are a few lakes which were formed by glacial scouring. These lakes are fairly deep, elongate, and oriented in a westerly direction, or generally in relation to past glacial flow which has been very active within the past 100 years (Tarr and Martin 1914).

Deposits of glacial till, silts, and sands are abundant along the braided channels of the Bremner River. The lower reaches are characterized by broad sand bars and poorly defined channels. Beds of "quicksand" were found along most of the river adjacent to the study area.

The Bremner area has a climate intermediate between continental and oceanic. Temperatures may reach a winter minimum of –30 F and a summer maximum of 80 F. Evidence in the form of blazes and cut branches suggests considerable snowfall during the winter months.

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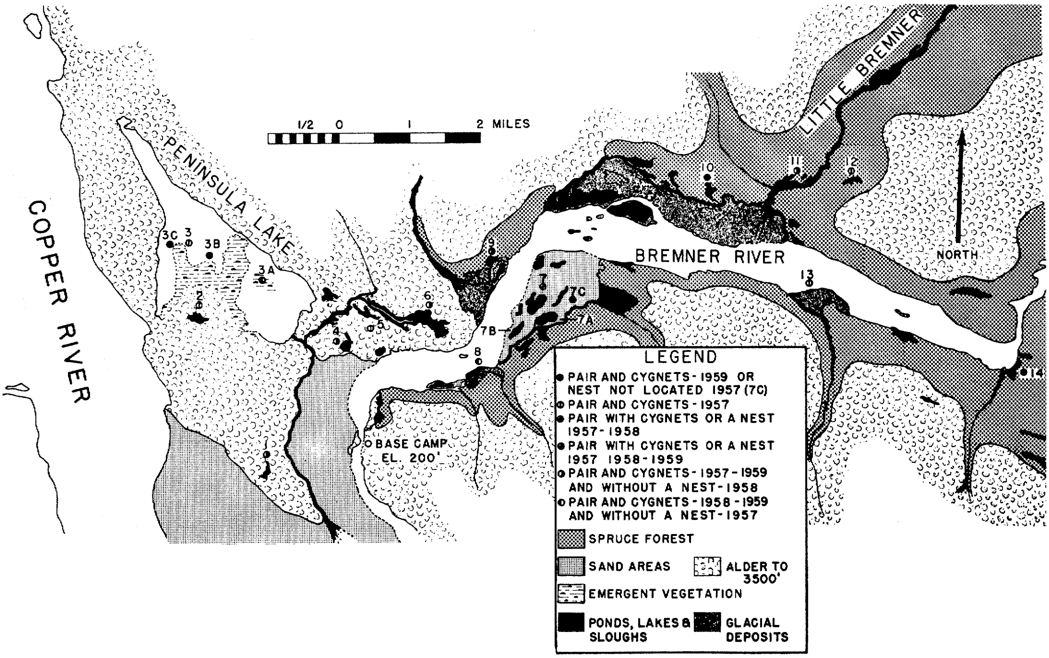

FIG. 2. Map of Bremner River study area showing trumpeter swan nest sites, 1957–1959.

A persistent wind condition, aggravated by the funnel effect of the Copper River Canyon, occurs on the Bremner River during both winter and summer. The winter winds are produced by cold, dense air masses moving down the Copper and Bremner rivers from the interior of Alaska towards the warmer coastal areas. Broken and splintered trees reflect the destructive force of these winds on the local vegetation. The wind situation is reversed during the summer when the warm, rapidly rising air of interior Alaska combine with convection currents from vast sand areas near the mouth of the Bremner River to draw cool air masses off the ocean 50 miles to the southwest (Fig. 3). These winds usually begin at mid-morning and occasionally reach velocities of 50 to 60 miles per hour by late afternoon. They cease abruptly in the cool of the evening. Silt and sand particles from the river bars billow up into a dust cloud which often reaches 3,000 ft in altitude. Deposits of these windborne materials are evident in the local ponds. Large dunes in this area are stabilized by stands of alder (*Alnus crispa*) (Fig. 4).

The terrestrial vegetation reflects the interaction of climatic, topographic, edaphic, and zootic factors. Stands of Sitka spruce, white spruce (*Picea glauca*), and hemlock cover much of the well-drained and less precipitous hillsides to elevations ranging from 2,500 to 3,000 ft, depending on exposure (Fig. 5). Thickets of alder occur up to 5,000 ft. At the mouth of the Bremner River, and for a few miles upstream, alder grows from the river bottom to 4,500 ft on steep talus slopes which appear to receive a heavy snowpack, as evidenced by the down hill slant of the shrubs. Birch (*Betula nana*) is also associated with the spruce–hemlock forest at lower altitudes, and balsam poplar (*Populus tacamahaca*), as well as black cottonwood (*Populus tricocarpa*), appear along raised gravel bars and the edges of some lakes and streams.

Mosses, western bracken (*Pteridium aquilinum*), common horsetail (*Equisetum arvense*), Lyall nettle (*Urtica lyallii*), wild

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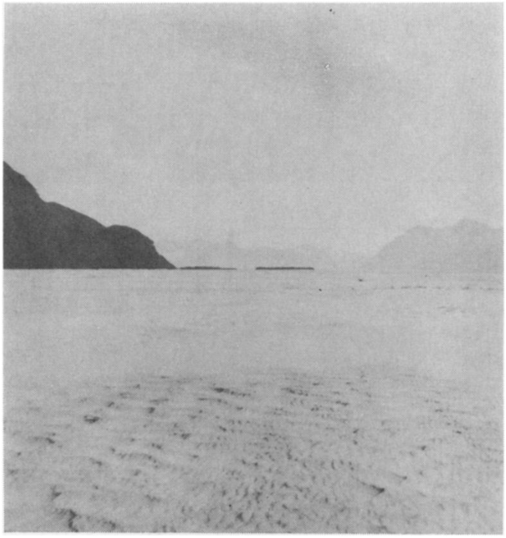

FIG. 3. Extensive sand area at the confluence of the Bremner and Copper rivers. (Photo by Shepherd)

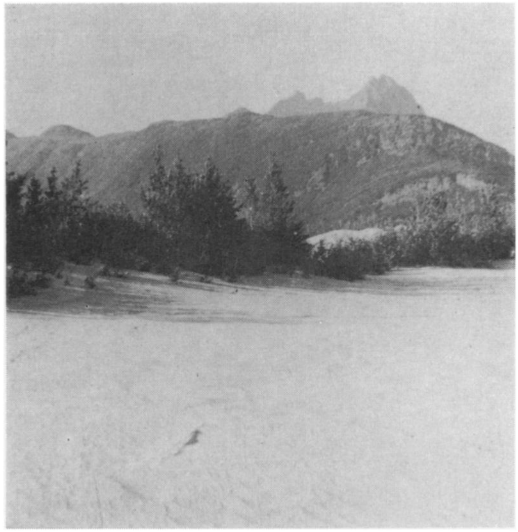

FIG. 4. Sand dunes on the Bremner River stabilized by *Alnus crispa*. (Photo by Shepherd)

rose (*Rosa* spp.), devil's club (*Oplopanax horridus*), red-berries elder (*Sambucus racemosa*), and highbush cranberry (*Viburnum edule*) are common understory plants associated with the spruce–hemlock forest.

Horsetail, nettle, devil's club, and wild celery (*Heraculeum lanatum*) are the most common plants found in the alder thickets, both on the river banks and the mountain sides.

Bare, rocky stream banks and glacial deposits support scattered clumps of Nootka lupine (*Lupinus nootkensis*), fireweed (*Epilobium latifolium*), alder, and willow (*Salix* spp.) (Fig. 6).

Copper River Delta

The Copper River Delta is a flat expanse of glacial and alluvial deposits formed by the Copper River and numerous, adjacent glacial streams which discharge into the Gulf of Alaska at contiguous points. These flats lie immediately east of Prince William Sound from Point Whiteshed eastward along the shores of the gulf for approximately 50 miles to Cape Martin. Fronting the entire shoreline of the delta at a distance of 4 to 7 miles offshore is a single line of low, sandy islands. An extensive shallow embayment, sheltered from the open ocean, lies between the shore and these islands. The terrain rises imperceptibly from sea level, beginning on the mainland shore of this intertidal bay and extending inland to the surrounding mountains 7 to 10 miles distant.

The climate varies little from that of Cordova, situated just west of the flats, except that, winter winds funnelling down the Copper River lower the maximum spring temperatures enough to retard snow and ice melt on the eastern part of the delta. There is a visible line of demarcation between this frozen area and that of the delta west to Cordova. This phenomenon is evidenced by a delay of 7 to 10 days in the spring phenology of the eastern section.

The terrestrial vegetation of the delta may be segregated into 5 communities: (1) *Elymus*; (2) *Carex*; (3) *Alnus–Elymus*; (4) *Alnus–Salix*; and (5) *Picea–Tsuga*. Nesting areas of the trumpeter swans associated with the *Alnus–Elymus* community

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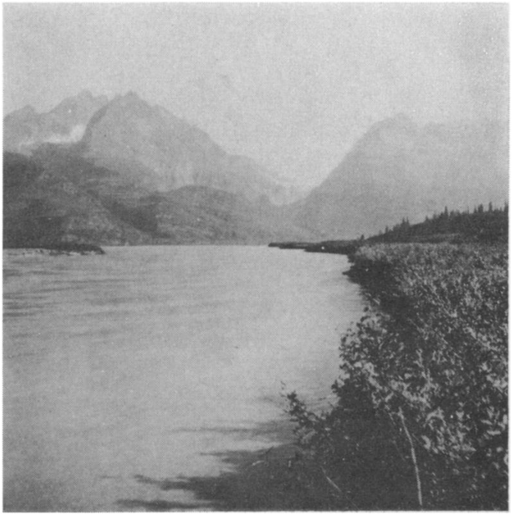

FIG. 5. View of the Bremner River from the field campsite. Note rugged topography and glaciated valleys. (Photo by Shepherd)

FIG. 6. Abandoned river channel of the type which provided some of the nesting and brood lakes. (Photo by Shepherd)

are restricted to the large sand islands in the main channel of the Copper River. At this point the river is braided, 6 miles wide, and terminating in a broad estuary, largely comprised of intertidal flats. The islands rise from the sealevel flats to a maximum height of 122 ft in the form of large sand dunes. The most conspicuous vegetation established on these large ridges of sand is composed of alder, beach rye grass (*Elymus mollis*), and black cottonwood. Lowlying areas between these dunes are occupied by shallow, clear-water ponds.

About 3 miles inland from the sedge flats of the inshore tidal area, a community dominated by alder and willow forms the dominant vegetation. This cover is distributed across the upper, or most inland, reaches of the flats and forms a broad ecotone with the spruce–hemlock forests of the buttressing mountains. This area is interrupted by fewer sloughs and ponds than the sedge flats. Stands of cottonwood are commonly found associated with this cover.

Generally, most of the ponds where considerable swan nesting occurs are found within the *Picea–Tsuga* and *Alnus–Salix* communities. This is especially true east of the Copper River where most of the swans nest. The ponds and lakes on this portion of the flats have resulted largely from glacial action and beaver activities.

The epicenter of the earthquake that rocked all of south-central Alaska on 27 March 1964 was located near the Copper River Delta. As a result of the quake the delta was uplifted with respect to the sea by as much as 1.89 m (Reimnitz and Marshall 1965). An abrupt physical change of this magnitude would cause significant ecological changes in a short time. Among the scientists who became interested in documenting these changes, Crow (in press) produced an excellent and much more detailed study of the ecology of the Copper River Delta than presented herein. Furthermore, where differences appear between Crow's description and ours, his will supersede these.

Kenai Peninsula

The Kenai Peninsula is divided into 2 distinct geographic features. The Kenai Mountains which rise to 6,000 ft and their

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foothills constitute the greatest portion of the Peninsula. Lying westward of these mountains and surrounded by Cook Inlet are the vast, flat lowlands covered with a spruce–birch–aspen type forest interspersed with many muskegs, streams, and dotted with over 1,000 lakes. This lowland area, most of which is within the Kenai National Moose Range, consists of approximately 1,500,000 acres. Numerous burns over much of this area have resulted in a succession largely dominated by fireweed, cottonwood, birch, and extensive stands of grass, largely *Calamogrostis* spp.

The climate is characterized by cool, cloudy summers and cold winters with temperatures falling to –30 F in winter and rarely exceeding 75 F in summer. The annual precipitation is 19 inches.

Most of the smaller lakes become ice free by the middle of May and freeze again by mid-October.

METHODS

Both species of swans native to North America, the trumpeter swan and the whistling swan (*Olor columbianus* (Ord.)), are summer residents of Alaska. In fact, a major portion of the whistling swan breeding population occurs in Alaska and the breeding range of the 2 species overlaps to some extent near the Bering Sea coast. This necessitated a means of field identification to differentiate the species in order to determine the population status of the trumpeter swan.

Identification of Swans from the Ground

Ornithologists and taxonomists have clung to the notion that postmortem examination of the trumpeter swan is the only positive means, other than voice, by which this species may be distinguished from the whistling swan. Obviously, it is impractical to identify the trumpeter swan by autopsy and field workers have been hampered by a good external means of reliably separating the species for more than a century. With the exception of the voice criterion, 3 methods of identification based solely on external characteristics were used in the past: (1) tail-feather count; (2) bill coloration; and (3) measurement of various bill features (Banko 1960).

An erroneous impression that trumpeter swans possess 24 tail feathers developed from a casual remark by John Richardson, but this was later clarified by Stejneger (1882) as an inconsistent and unreliable character (Banko 1960). Field examination of 48 adult and subadult trumpeter swans in Alaska revealed that the number of rectrices ranged from 20 to 24, with a mode of 22. These observations substantiate the view of others concerning the nonreliability of this criterion as a diagnostic field characteristic. We agree that such an unreliable method of identification should be discarded.

Bill coloration is another source of conjecture. Earlier writers and taxonomists referred to the posterior area of the maxilla immediately in front of the eyes, known as the "lores," as a diagnostic character. In the whistling swan this area usually is charcterized by a "tear drop" spot of yellow or orange-yellow, although in some individuals this mark is entirely absent. In contrast, the bill of the trumpeter swan should be entirely black, but this rule is not absolute. Banko (1960) cited such anomalies as olive-yellow spots in the loral region of trumpeter swan, as well as a small indistinct gray spot of irregular shape behind the nostril. We have noticed no colored lores in trumpeter swans observed in Alaska, but possibly they were overlooked. It seems, then, that swans with completely black bills may be of either species, whereas those with a bright yellow or orange-yellow spot on the lores are definitely whistling swans.

Another uncertain characteristic pertaining to bill coloration concerns the salmon-red streak on the mandible. Kortright (1943) stated that the trumpeter swan's bill is "black, with a narrow salmon-red streak on the edges of the mandibles, lacking in

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FIG. 7. Fledged trumpeter swan cygnet illustrating the straight profile from crown to nail and heavy development of the culmen. (Photo by Shepherd)

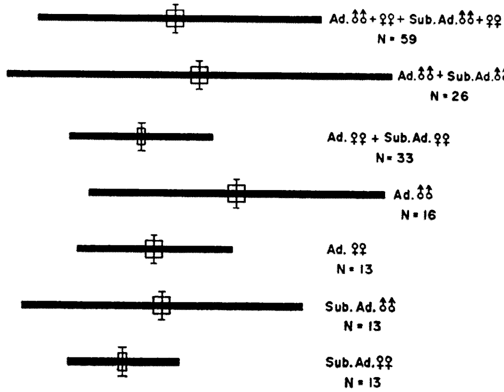

FIG. 8. Statistical comparison of nostril to nail measurement.

the Whistling Swan." Banko (1960) stated: "My experience not only demonstrated that the salmon-red streak on the trumpeter was confined almost wholly to the basal section of the lower mandible edge, but that there was great variation in the degree to which it is present." We agree with Banko's statement and, in addition, have observed whistling swans with both a yellow lore spot and a salmon-red "grinning" streak on the mandible. Thus, it appears that this character should also be eliminated as a positive diagnostic feature.

Delacour (1954) mentioned a difference in the profile of the culmen between the 2 species. We also observed, in the field, that the whistling swan possesses a concave culmen, whereas the trumpeter swan's culmen appears heavier and nearly straight, even at an early age (Fig. 7).

Various bill measurements furnish another distinguishing feature, especially the position of the nostril in relation to the bill length (Stejneger 1882). Because there are obvious overlaps in measurement between large whistling swans and small trumpeter swans, it is necessary to establish limits to the bill measurement which are used as a diagnostic index. Apparently, the most reliable measurement is the distance from the anterior edge of the nostril to the tip of the bill nail. This measurement was taken with a vernier caliper and read to the nearest tenth of a millimeter.

The mean of this bill measurement from 59 adult, 2-year, and yearling trumpeter swans on the Copper River was 54.1 mm. Approximately 95% (2 standard deviations) of this population had a nostril-to-nail measurement greater than 49 mm and less than 59.2 mm (Fig. 8). The same measurements given for whistling swans by Banko (1960) show an extreme of 49 mm. Thus, Banko suggesed that "when the voice and bill color characters of a given swan are missing or in doubt, any swan over 1 year of age, of either sex, which measures 50 mm (2 inches) or more from the tip of the bill to the front edge of the nostril, probably is a trumpeter swan. If the subject measurement is less than 50 mm, identification of the species as a whistling swan is most likely to be correct."

The regression illustrated in Fig. 9 suggests a differential relationship between body weight and bill measurement of male and female trumpeter swans, at least in the population from the Copper River. The slope of this relationship for males was calculated as +.269 and the females as

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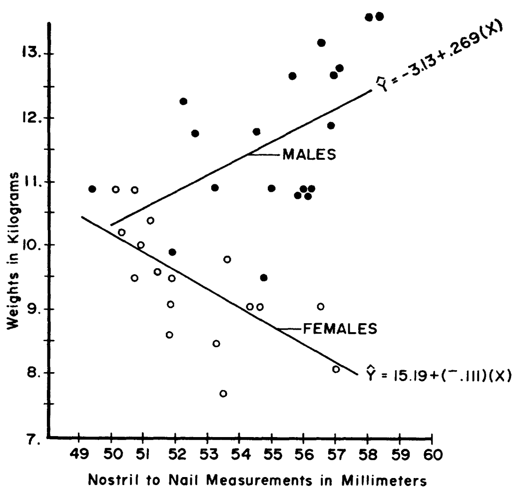

FIG. 9. Regression of body weight over nostril-to-nail measurement in trumpeter swans.

–.111. A statistical test was made to determine if these 2 groups of data could be combined. Clearly, the highly significant (**) F value precludes grouping. Of further note is the source of the difference, i.e., is it because of a difference in adjusted means or in slopes, or both? These were also tested statistically (Table 3).

The resulting values of F are highly significant (**) and indicate that there is a real difference between the adjusted means and between the slopes of the regressions for male and female trumpeter swans. The difference between adjusted means suggests that a male with the same bill measurement as a female will differ significantly in body weight. Moreover, the difference between slopes suggests an inverse relationship in body weight over bill measurements for females; i.e., female bill measurements are not dependent on body weight. Further analyses of these data show no correlation between the age of the female and the observed slope. Banko (1960) stated that various bill measurements are dependent on size. This is verified by the male regression (correlation coefficient of .545) but not by the female regression (correlation coefficient of .206). The former is significant at the

TABLE 3.—ANALYSES OF BILL MEASUREMENTS IN TRUMPETER SWANS. THOSE MARKED WITH A DOUBLE ASTERISK(**) ARE HIGHLY SIGNIFICANT

Source	Errors of Estimate df	SS	MS
Part A			
Deviations from overall regression	34	69.6	
Deviations from individual regressions	32	25.3	.79
Difference	2	44.3	.79
$F(2.32) = \frac{22.1}{.79} = 27.9^{**}$			
Part B			
Deviations from overall regression	34	69.6	
Deviations from average regression	33	36.5	1.1
Difference	1	33.1	1.1
$F(1.32) = \frac{33.1}{1.1} = 30.10^{**}$			
Part C			
Deviations from average regression	33	36.5	
Deviations from individual regressions	32	25.3	.79
Difference	1	11.2	.79
$F(1.32) = \frac{11.2}{.79} = 14.77^{**}$			

95% level, but not the latter. However, the sample was small and conclusions may be only tentative at this point.

We relied heavily on a fourth method of identification to determine trumpeter swan nesting distribution. This was egg measurements wherever nests could be reached (Fig. 10), the results of which are described in detail under "Breeding Biology."

Identification of Swans from the Air

Nesting investigations on the Bremner River during the summer of 1957 suggested a possible criterion for identifying swans at their nest sites from the air. This involved identification of the "moat" which surrounds most trumpeter swan nests. The birds remove vegetation for nest material

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FIG. 10. Identification of trumpeter swan eggs on a marsh near the outlet of Tyone Lake. This was the "discovery nest" in the Gulkana Basin that verified the trumpeter as the resident species of swan in this area. (Photo by King)

in a large circular area and heap it in the center of the circle. The nest is almost always constructed in emergent vegetation away from the shoreline so that from the air the whole structure gives the appearance of a huge "donut" with the nest itself being the hole (Fig. 11) (the details of nest construction are given in the chapter on "Breeding Biology"). In contrast, whistling swans prefer upland nest sites, or at least dry locations not associated with emergent vegetation, although they usually nest close to water (Fig. 12). A whistling swan nest appears to give the profile of a volcanic cone whereas the trumpeter nest resembles a bulky, round haystack. Nest site and type has been the criterion used to identify the occasional trumpeter swan where the range of the 2 species overlaps. Basically, however, the trumpeter swan is a boreal species and the whistling swan an inhabitant of the open tundra.

Aerial and Ground Study Techniques

Aerial Surveys

Swan studies in the lower Copper River Basin were, of necessity, divided into 2 phases: (1) aerial surveys, and (2) detailed ground studies. The aerial census technique basically consisted of a system-

FIG. 11. A typical trumpeter swan nest built in emergent vegetation. Two trumpeters sit beside a nest containing 5 eggs in rank *Equisetum* growing in water 30 inches deep. Note the previous year's nest in the lower right corner. (Photo by Hansen)

atic search of all available swan habitat. These surveys were conducted with 5 major purposes in mind:

1. To determine the approximate breeding population of swans in south-central Alaska initially, and eventually, throughout the trumpeter swan breeding range in all of Alaska;
2. To secure as many complete brood counts as possible;
3. To determine the ratio of breeding swans to paired nonbreeding adults and adults in flocks;
4. To make a reconnaissance of potential study areas and habitat types, and to locate specific nest sites for subsequent ground study;
5. To extend nesting studies to areas inaccessible from the ground.

Aerial surveys were conducted over suitable swan habitat using Piper Supercub and Cessna 180 aircraft. Nest sites and

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FIG. 12. Typical whistling swan nest on a dry site near a tundra lake on the Yukon–Kuskokwim Delta. (Photo by C. J. Lensink, Bureau of Sport Fisheries and Wildlife)

flocked swans were located by cruising at 500 ft. The aircraft was then flown at a lower altitude to count cygnets or yearling swans, identifiable by their darker plumage.

Eggs in uncovered nests were counted by making a slow pass 10 to 20 ft above the nest. This technique appeared to disturb the swans only temporarily, if at all. In fact they frequently displayed a defensive posture toward the airplane.

Swans are easily located because: (1) their color contrasts conspicuously with the vegetation; (2) trumpeter swans have conspicuous nests; and (3) they tend to concentrate, when molting, in flocks on large lakes. Some disadvantages were encountered while flying census surveys on bright, sunny days over lakes whose surfaces were dappled by wind action. The reflections of sunlight from choppy water prevented accurate observations. As with other waterfowl, partially overcast days with little or no wind were best for aerial censusing of swans.

In an effort to determine if all the swans censused in south-central Alaska were trumpeters, much of the area covered by air was also reconnoitered on the ground, where possible. Over a wide geographic area swans were captured for banding and measurements were obtained of swans and swan eggs. These observations showed that the resident breeding swan populations of this geographic area were trumpeters. We assumed that any whistling swans occurring on the breeding grounds of the trumpeter swans were birds that dropped out of migrant flocks and did not nest successfully, if at all. Where the 2 species overlap, it is the trumpeter intruding into the whistling swan breeding range near

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the Bering Sea coast, and not the whistling swan extending to the interior.

A banding crew working on the Copper River Delta in July 1955 saw 2 flightless, nonbreeding swans. One was caught and identified as a whistling swan. Another possible summer record of a whistling swan on the Bering River Flats in 1955 was obtained by Dr. George E. Hudson (pers. comm. 1960), who caught a small, flightless swan, which he tentatively identified as this species. Of some 190 swans captured for banding within the breeding range of the trumpeter between 1957 and 1968, however, only 2 were identified as whistling swans. One was captured on a large lake atypical of trumpeter habitat in the Tanana Valley south of Fairbanks and the other on a large lake near Tetlin in the upper Tanana Valley.

FIG. 13. Dense stand of *Equisetum fluviatile* in 18 inches of water. Man in center is 5 ft 6 inches tall. (Photo by Shepherd)

Ground Studies

The lack of roads and the vast distances encountered in Alaska pose many logistic problems for the field worker. For this reason, much of the transport work necessary during the investigations was accomplished either with a Grumman Goose or Cessna 180 aircraft. Small boats, food, personnel, and scientific equipment were flown from Anchorage to base camps on the Bremner River and the Copper River Delta.

Nest sites were visited on the ground by using a number of conveyances. Among these was a 16-ft, square-stern Fol Boat, used on the Bremner River, which proved rather fragile for navigating the turbulent glacial waters. A 13-ft Grumman aluminum canoe aided in reaching remote beaver ponds and sloughs. The canoe was portaged from the river into ponds frequented by swan families. A few areas could be reached only on foot. A float plane was used to reach many remote nest sites on lakes large enough to land and take off.

Observations of swans with young were usually made with binoculars or with a 20-power spotting scope. Areas in which swans were present had to be approached carefully, because the birds were extremely wary and, upon sighting a person, immediately concealed themselves in the rank vegetation. Various vantage points for observation at each nesting site were established when possible. This proved most successful, since few complete brood counts, or behavioral observations, were secured unless the swans were completely unaware of human intrusion.

Travel in the ponds along the Bremner and Copper rivers was restricted by the dense emergent vegetation common to most of the shallow, confined waters of these areas. This vegetation, in turn, benefited the swans and many took full advantage of the excellent concealment it provided. Some ponds contained such dense vegetation that a boat could not be used, and many ponds were nearly impossible to wade (Fig. 13).

Plant Surveys

Analyses of the aquatic plant communities indigenous to the hydrosere of the Bremner area were accomplished during the summers of 1958 and 1959. Plant tran-

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TABLE 4.—TRUMPETER SWANS BANDED IN ALASKA, 1957–1968

	Adult			Yearling			Cygnet			
Year	M	F	?	M	F	?	M	F	?	Total
1957	1	2					15	13		31
1958	6	3		3	2		9	7[1]	1	31
1959	4	8		5	2		8	6		33
1960	7	22	13	11	5	8	4	3		73
1962			2			1				3
1966		2								2
1967		4					4	4		12
1968				1						1
Total	18	41	15	20	9	9	40	33	1	186

[1] One of these found dead on 15 December 1959 at the mouth of the Nanaimo River, British Columbia, and reported as a Canada goose.

sects were established in 10 lakes of varied physical and vegetational composition. Each transect consisted of 50 one-decimeter-square plots placed at 0.5-m intervals along a 25-m cord line. An attempt was made to pick relatively homogenous plant cover (primarily to avoid ecotones). Therefore, nearly all transects were run parallel to the shoreline. The occurrence of each plant was recorded on a frequency basis only if stems of these plants were within the plot area. The data from the 80 transects established on the Bremner River are summarized in Appendix III.

In connection with the analyses of the aquatic plant communities, a limited study of the associated flora and fauna and the chemical and physical properties of the ponds was made. These studies consisted of insect collections taken in the emergent vegetation, plankton hauls from the open water, *p*H determinations, water temperatures, and turbidity tests. Five ponds were completely mapped to: (1) delineate the various successional stages encountered on different habitats, (2) show graphically the trumpeter swan cover and nesting requirements, and (3) illustrate the morphology of these water areas. The method used to map these ponds was the "two-point resection" techniques described by Welch (1948). Limnological techniques and terms follow those of Welch and of Hutchinson (1957).

Prior to the qualitative habitat studies, 61 species of plants were collected for later identification and subsequently deposited in the University of Alaska and Washington State University herbariums (Appendix V).

Color Marking and Banding

In order to fulfill some of the objectives of the swan study, considerable emphasis was placed on banding and marking techniques in the early stages. A combination of 3 techniques was used: metal leg bands, plastic neck bands, and color marking of plumage.

Leg Banding.—Banding was conducted most intensively in the summers of 1957 through 1960 in the lower Copper River Basin. During that time 168 swans were banded including 66 adults, 28 yearlings, and 65 cygnets. In the following years of the study, an additional 18 trumpeters were banded elsewhere in south-central Alaska (Table 4).

During the banding operation on the study areas, an attempt was made to investigate every known pond frequented by broods and all large lakes that molting swans were known to inhabit. Once a brood was located, care had to be taken not to alarm the swans. If the birds detected the banders' approach, they slipped quietly into dense emergent vegetation and concealed themselves.

Because hand capture seemed reasonably effective, traps were not used, although they could possibly be utilized under certain conditions. The most satisfactory method was that of pursuing molting adults and cygnets in open lakes or ponds with an outboard-powered boat. Swans chased in this manner tired quickly, and generally could be caught within a few minutes. A long-handled, large dip net helped. Where large concentrations of molting adults were encountered, each captured bird was dyed with purple to eliminate the chance of repeatedly chasing the same individual.

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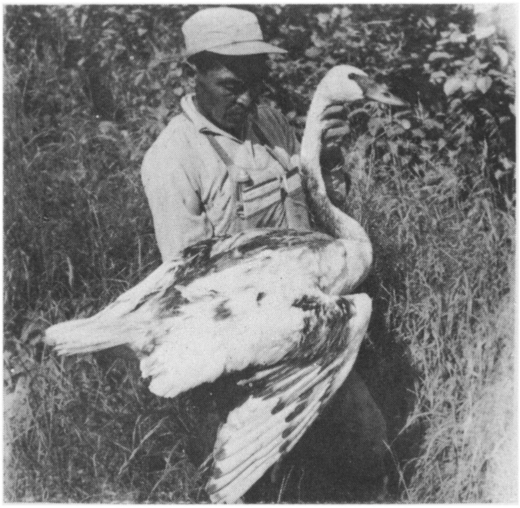

FIG. 14. Purple dye proved unsatisfactory as a means for sight identification of adult swan. Too frequently color-marked adults were indistinguishable from gray plumaged cygnets at a distance. (Photo by Shepherd)

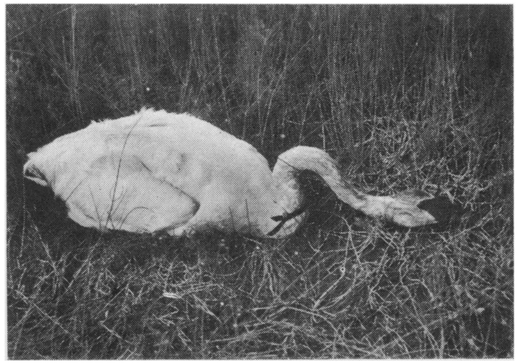

FIG. 15. Flightless adult female trumpeter swan marked with black, vinyl plastic neck band. The tassels, cut short for the safety of the bird, limited the usefulness of the marker which was easily buried in the plumage and not visible. (Photo by Shepherd)

A standard, size 9 band would not remain on a cygnet's tarsus if the swan was less than 3 weeks old. From this standpoint the best period for banding was when the cygnets were about 8 weeks old. However, after 5 weeks of age, the young became more active and rather difficult to catch in the rank vegetation. Experience demonstrated that the standard size 9 band was too small for adult male trumpeter swans. Consequently, a stainless steel, hand-stamped, lock-on band was used for most of the banding after the first year. These bands appeared to be satisfactory and should wear for the life of the individual bird even though it spends much of its long life in brackish or corrosive sea water.

Color Marking.—During the 1958 and 1959 field studies, 2 types of purple dye were used to mark trumpeter swans, a solution of 50% alcohol mixed with rhodamine b and malachite green (Kozlik 1956), and a commercial ink applicator known as "Magic Marker" type A. The first solution was entirely unsatisfactory because it usually washed off when the birds were released, although one swan retained a purple stain on various parts of its plumage 6 weeks after marking. Less fading was noted with the Magic Marker and areas from which the feathers had not molted were still bright after nearly 2 months. Some birds were recovered the following year with traces of this dye still visible.

Although hindsight proved purple to be a poor choice, 42 swans were color marked (14 adults, 8 two year olds, 15 yearlings, and 5 cygnets). In retrospect, a bright color should have been used inasmuch as swans dyed with purple were extremely difficult to see while on the water. Moreover, a cygnet's natural plumage was nearly the same shade as the purple in poor light and some of them might have been confused with colored adults (Fig. 14).

Neck Banding.—Because neck bands offer an excellent means by which individual birds or particular age groups may be identified (MacInnes 1966), a limited program of this type of marking was initiated in 1958. Neck banding of swans in western Canada at that time precluded any extensive marking of this type in Alaska to avoid possible confusion. Nevertheless, black, yellow, and red neck bands of ½-inch wide

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vinyl plastic were placed on 5 adults, 3 yearlings, and one cygnet. A jesse knot was used to secure these bands. Tassels were cut short in order to prevent possible ice accumulation in winter (Fig. 15).

We had hoped that information from color marking would provide enough observations to justify marking swan populations with numerous colors in the future to show whether or not exchange occurs between Alaskan swans and those of other breeding areas. We were also interested to see if the wintering range could be identified or perhaps delineated by this method of identification.

ECOLOGY OF THE TRUMPETER SWAN NESTING HABITAT

The form of a lake or pond basin and the body of water that occupies it depends partly on the forces that produced the basin and partly on events that follow within the lake or pond. The biotic development of a bare area is a reflection of the forces which formed the pond or lake and of the basin morphology. The development of a pond or lake is, to an extent, dependent on its vegetative growth, although there is a complex of interrelated factors involved between the development of an aquatic flora and the physical environment.

If the character of the plant community results from all factors, the vegetation is an indicator of the ecosystem. Although one is unable to detect finite changes in soils, exposure, etc., he is able to see these changes reflected in plant distribution. However, every component of the vegetational mosaic is not an indicator of the ecosystem. More important are those plant communities that are repeated on particular habitats. The location of these plant communities gives clues to the nature of the factors controlling their establishment.

The previous summary of the climate and geology of the study areas should suffice as a background for consideration of the physical environment, its origin, morphology, maintenance, and longevity. These physical features are the primary or intrinsic factors behind the development of the local hydrosere in the Lower Copper River Basin.

Physical Factors

Origin of the Water Areas

Exact determination of the origin of each of the ponds and lakes encountered on the Copper River study areas is problematical. However, some factors recognized in the formation of pond areas are fluviatile, zootic, glacial, and eolian. Water action appears to be the foremost creative force in the development of bare areas.

Three types of lakes are characteristic of the lower flood plains of south-central Alaska: (1) oxbows, (2) lakes in abandoned channels or scours, and (3) lateral levee lakes. The oxbow, usually is formed when a river meander bisects part of its downstream channel, thereby leaving a loop in the shape of an "oxbow." Typically, oxbows in this area are deep (8 to 15 ft), eutrophic, and closed from the main river by a levee of silt or often the dam of a beaver (*Castor canadensis*). The water of these lakes becomes clear as the silt settles out and is generally warmer than the adjacent river.

The majority of rivers draining glaciated regions carry an abnormally heavy load of sediment in suspension, due to the scouring action of the moving ice field. Therefore, large rivers carrying these loads of sediment tend to deposit levees or natural dikes delimiting their natural channels. This tendency results from the difference in currents from one side of a river to the other. Turbulence is often insufficient along the quiet marginal waters to keep a considerable part of the sediment in suspension. If this deposition occurs at high water stages, these sediments may be left as a levee, bank, or wide bar (Hutchinson 1957).

Subsequent high water levels may scour channels through these areas, forming numerous elongate, shallow pools (Figs. 16 and 17). Rarely are these basins found to

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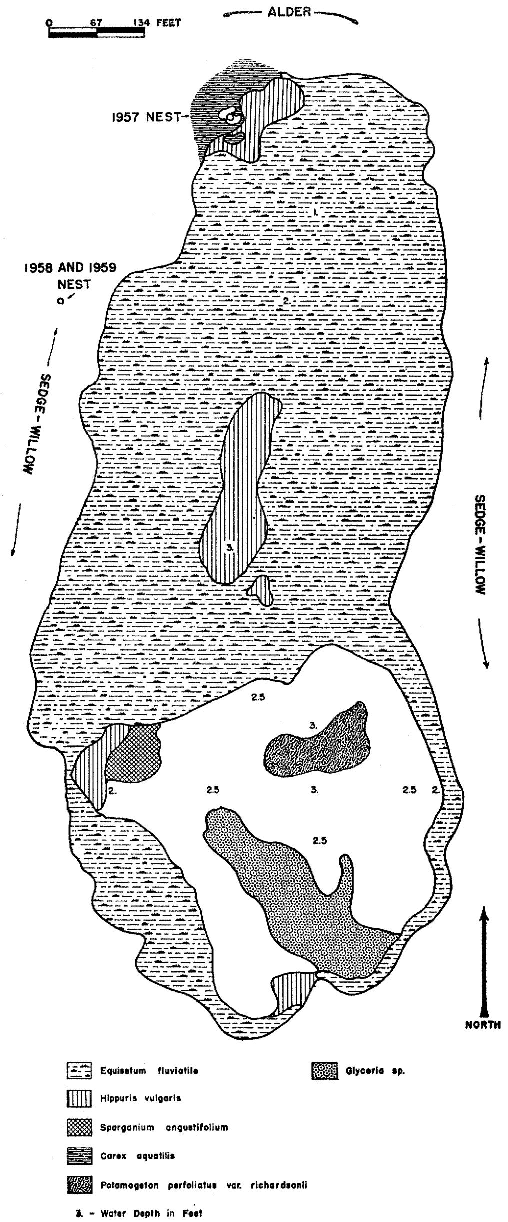

FIG. 16. Cover map of Pond 7 drawn from a plane table survey.

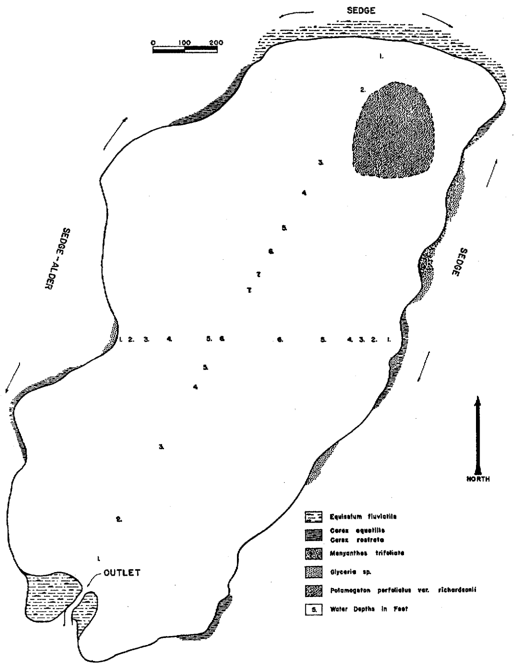

FIG. 17. Cover map of Pond 7a drawn from a plane table survey.

exceed 6 ft in depth, and most are 3 to 4 ft deep. Since they are formed in rich silts, the ponds tend to be eutrophic, and vegetative development appears rapid. Water levels are surprisingly stable, considering the fact that few of these basins have outlets. High water levels are only temporary and occur in the spring with the melting of the snow. Evaporation is slow and rarely causes a great drop in water level.

The third type of pond or lake formed by river action, the lateral levee, results from the preceding conditions when the river runs close to the edge of its flood plain, which is often delimited by a scarp or terrace. The basin formed by the levee on the stream bank and the adjoining scarp collects water and becomes a pond or lake of variable depth.

Many of the ponds encountered in the study resulted from beaver activity (Figs. 18 and 19). Most often, beavers had dammed clear streams forming small ponds of 6 to 15 acres. Some ponds were merely former oxbows, sloughs, or river channels dammed by beaver. Still others were lakes or ponds with small outlets that the beaver had blocked. As a result of this activity, water levels of these ponds were kept more

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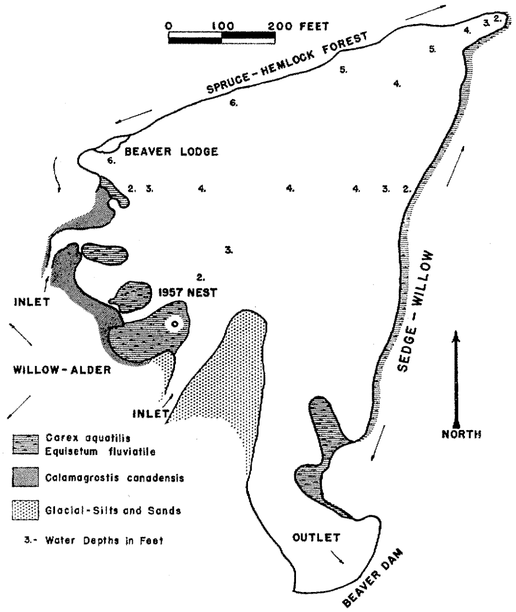

FIG. 18. Cover map of Pond 9 drawn from a plane table survey.

or less stable. The range in the depth of beaver flowages varied, depending on the origin, source of water, and the age of the pond.

A number of lakes and ponds originating from glacial action were evident on the study areas. The majority of these were kettle like and remained on the outwash aprons of the deglaciated areas. A few resulted from glacial meltwater filtered through the gravel. Kettles and meltwater basins were used extensively as trumpeter swan nest sites on the Martin and Bering river flats. These water areas tended to be somewhat oligotrophic and deep, and in consequence supported different vegetation than those encountered in the shallow, eutrophic ponds formed by river action. Lakes and ponds created by ice scouring were seldom used as nest sites by the swans. Glacial outwash plains are characterized by a high water table generally moving outward from the face of the glacier through coarse sediments which filter out suspended material. Thus, any depression is filled with clear water unless connected directly with a stream draining from under the ice face. Swans seek these clear waters.

The final force which formed some ponds and lakes on the Copper Delta is the wind. Eolian deposits of loess and sand on the estuary of the Copper River have formed a number of dunes. These dunes are dissected by depressions which are below the prevalent water table. Consequently, small lakes collect in these depressions. The morphology and vegetation of these ponds are similar to the shallow, well-vegetated basins upstream, although many have outlets dammed by beaver.

Morphology of the Water Basins

Certain morphometric parameters of ponds and lakes are of importance to ecologists because these parameters reflect the basins' morphology, origin, and history. Moreover, these data provide some information in regard to the existing plant communities. The parameters used in describing a few of the ponds and lakes occupied by trumpeter swans were: (1) mean depth (Z) obtained by dividing the volume of a lake by its area; (2) shoreline development (D_L), the ratio of the length of the shoreline to the length of the circumference of a circle of area equal to that of the lake, written as $D_L = L/(2\sqrt{\pi A})$ where A is the area; and (3) length of the shoreline (L) as measured on a map by a rotometer or a string (Hutchinson 1957).

The parameter D_L is based on a value of 1.0, which would represent a perfect circle. For instance, 4 circular basins just in contact would have a development of 2.0. The more irregular the shoreline, the higher value of D_L. The morphometric data from 6 basins in the Bremner River are given in Table 5.

Morphometric data for 11 ponds and lakes on the Martin River flats, calculated from topographic maps, were (1) area, 6 to 128 acres; (2) shoreline, 3,000 to 16,000 ft; and (3) approximate development of shoreline (D_L), 1.3 to 2.0. The average

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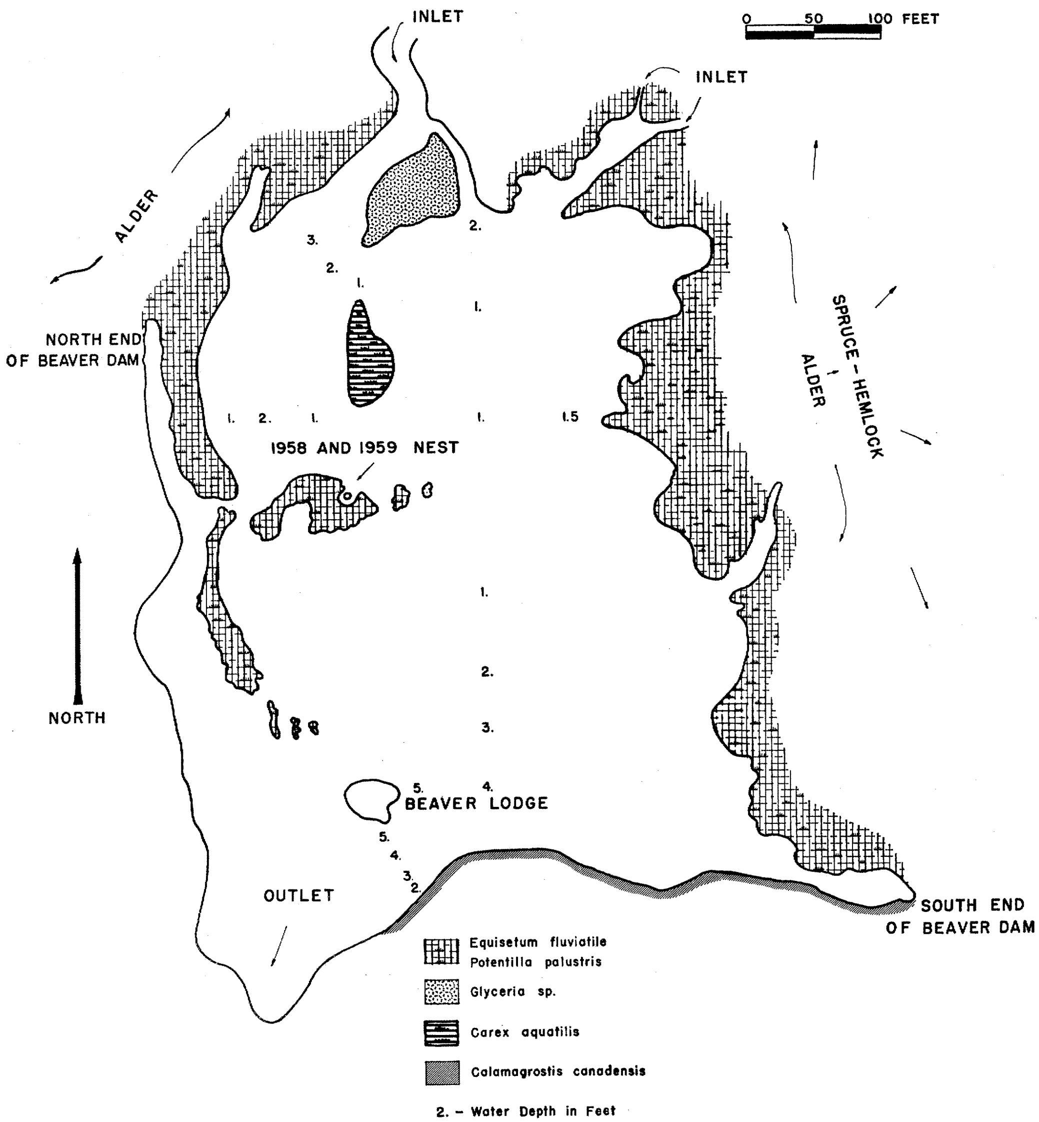

FIG. 19. Cover map of Pond 8 drawn from a plane table survey.

depth of these ponds could not be determined, but many were from 10 to 15 ft deep and would average well over 2 ft in depth.

Maintenance and Longevity

The existence of lakes and ponds depends on a number of processes that tend to form basins with a rim higher than the deepest enclosed point. Whenever there is sufficient water to fill such a depression, there is also the possibility of erosion. Therefore, the rim surrounding a lake starts to be destroyed as soon as it is created. This destruction is more rapid if the basin has an outlet or an inlet, which is often a charac-

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TABLE 5.—MORPHOMETRIC PARAMETERS OF 6 BASINS IN THE BREMNER RIVER STUDY AREA, ALASKA

Pond (no.)	Type[a]	Secchi (m)	Shoreline (ft)	Development of Shoreline (ratio)	Mean Depth (tenths of ft)	Area (acres)	Percentage of Area	
							Closed	Open
4	P	clear	4,059	1.7	1.7	10.0	86	14
7	RS	clear	3,550	1.3	1.5	14.0	76	24
7a	RSO	1.0 to clear	6,025	1.3	2.5	37.0	—	100
8	BP	.15	3,600	1.9	1.8	6.0	10	90
9	BP	.25	4,100	1.8	2.6	9.0	11	89
3	L	—	71,280	2.4	—[b]	1642.0	30	70

[a] P = pond; RS = river scour; BP = beaver pond; L = lake; RSO = river scour with outlet.
[b] Mean depth not determined.

teristic of lakes in areas of high precipitation. Meanwhile, sediments from shoreline erosion and those carried in by the inlet are deposited in the deeper areas of the lake. Likewise, the production of organic material is hastened as the basin becomes filled. Geologically, the lifetime of a lake is limited, but it may be prolonged by its inhabitants.

Activities of animals, especially beaver and muskrat (*Ondatra zibethica*), help control the growth of vegetation, retarding succession and creating bare areas. Beaver dams halt erosion and also settle silts, benefiting downstream locations. Even the swan is instrumental in delaying succession, through its feeding and nest building habits (Fig. 20). Open areas are maintained in many ponds largely by the scouring of food plants from the bottom by swans. Although the effects of these actions are only temporary, they briefly prolong the lifetime of a lake.

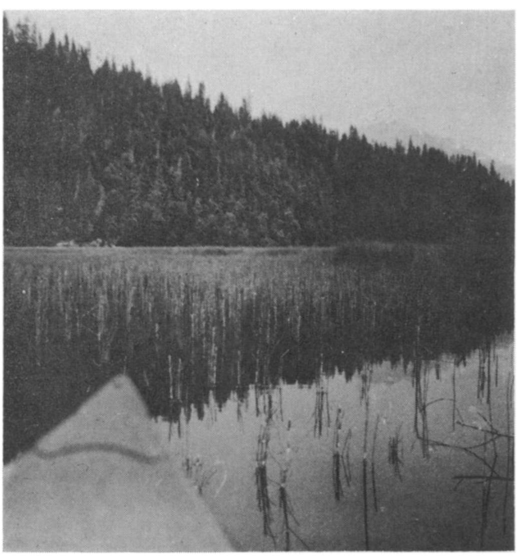

FIG. 20. Trumpeter swan feeding area in stand of *Equisetum fluviatile*. Note thinning and grazing effect from bow of canoe toward far shore. (Photo by Shepherd)

In addition, new habitat is being formed continually along the flood plains of the tributary streams and the main drainage system of the Copper River each year, as well as on the moraines of retreating glaciers. The activities of beaver are important in creating new areas. There is no reason to doubt that the present habitat will endure for many years, provided human disturbance is kept at a minimum.

Phytobiotic Complement

Types of Succession

The hydrosere of the lakes and ponds within the Copper River Basin is divisible into two distinct successions: (1) anchored mat, and (2) floating mat. The first type is characteristic of the shallow, eutrophic ponds which typify many of the water-, beaver-, and wind-created basins of the

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FIG. 21. Extensive floating mat community of *Menyanthes trifoliata*, Mile 28.5, Copper River Highway. (Photo by Shepherd)

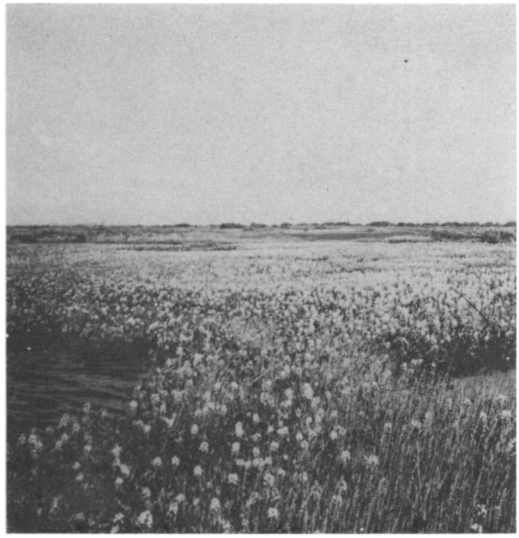

FIG. 22. *Menyanthes trifoliata* mat in bloom. (Photo by Shepherd)

Copper River. The shallow form of these ponds results in a broad littoral zone which is rapidly covered by a dense reed swamp (Fig. 13), dominated by *Equisetum fluviatile*, *Carex aquatilis*, and *C. rostrata*. *Potentilla palustris* and moss are associated with these genera in the seral stages which characterize the anchored mat. Other plants of lesser importance accompanying the mat stage of the sere include *Equisetum hiemale* var. *californicum*, *Eleocharis palustris*, *Eriophorum scheuchzeri*, *E. angustifolium*, *Juncus triglumis*, and *J. mertensianus*.

The remaining deeps, if any, are pioneered by *Potamogeton alpinus*, *P. perfoliatus* var. *richardsonii*, *P. pectinatus*, *Ranunculus aquatilis*, *Callitriche autumnalis*, *Myriophyllum* sp., and *Utricularia macrorhiza*. The most important seral genus is *Potamogeton*. Quiet, fairly open water areas are covered with *Lemna trisulca* and *L. minor*. The zone immediately between the emergent and the submerged vegetation is occupied by *Hippuris vulgaris*, *Sparganium angustifolium*, and occasionally by *S. minimum*.

The second type of succession, the floating mat, is peculiar to the deeper, slightly oligotrophic ponds and lakes formed largely by glacial action. Two genera are important in the formulation of these floating mats, *Menyanthes trifoliata* and *Carex* spp. Floating mats which extended well over 100 yards from the shoreline were encountered on the Copper River Delta and Martin River flats (Figs. 21 and 22). The early spring (May 15) aspect of this habitat is shown in Fig. 23. The open water beyond the mat vegetation was often occupied by compact stands of *Nuphar polysepalum*, *Potamogeton perfoliatus* var. *richardsonii*, and/or *P. pectinatus*.

Combinations of both types of successions were found on several of the ponds and lakes investigated during the study. No obvious reason for this differentiation was apparent other than the morphology of the basins. Generally, a steep shoreline gradient existed wherever there was an anchored mat or reed swamp.

Community Zonation and Development

Previous studies have demonstrated that water depth and light pentration are impor-

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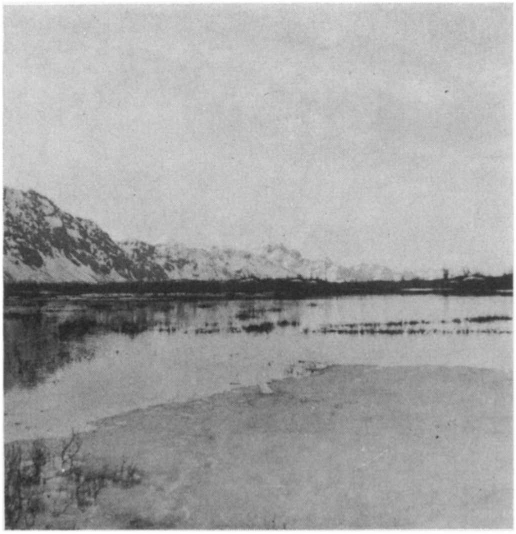

FIG. 23. Pregrowth aspect of floating mat community (15 May) pictured in Fig. 21. (Photo by Shepherd)

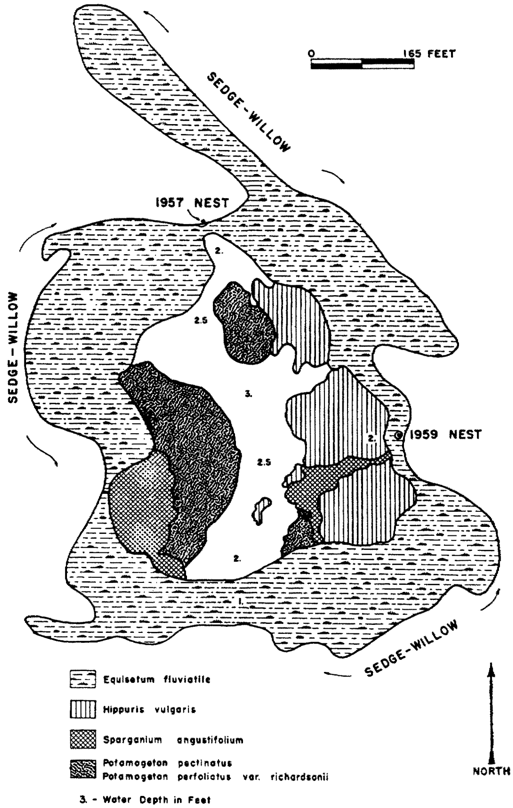

FIG. 24. Cover map of Pond 4 drawn from a plane table survey.

tant factors regulating early seral communities (Provost 1947). These factors are apparent in the data gathered during the course of this study as indicated by the relationship of water depth to establishment of plant communities (Appendix III). From this information, it is possible to segregate a number of seral communities constituting the hydroseres indigenous to the Bremner and Copper river areas.

The deep water community is composed of a number of species largely dominated by *Potamogeton perfoliatus* var. *richardsonii* and *P. pectinatus*. Genera associated with these species and of lesser importance were listed previously. This community is named after its most abundant occupant, *Potamogeton*, which occurs in water from 24 inches to more than 10 ft in depth. However, *Potamogeton*, *Ranunculus aquatilis*, *Callitriche autumnalis*, and *Utricularia macrorhiza* were seldom found, or at least were not abundant, in turbid ponds (secchi reading of 0.10 to 0.35 m).

With the accumulation of organic materials, eroded sediments, and windborne silts, the deeper areas of the ponds gradually filled and became suitable for establishment of the next community, designated *Hippuris/Sparganium*. It occupied the zone of water from 24 to 36 inches deep. The median depth inhabited by this community was 30 inches. The 2 main genera of this seral stage were accompanied by remnants of the *Potamogeton* community, especially *P. perfoliatus* var. *richardsonii*, *P. pectinatus*, and *P. alpinus*. *Callitriche autumnalis* and *Utricularia mertensiana* were also included. *Sparganium angustifolium* was seldom present in glacial waters. Stands of this community are shown in Fig. 24.

A fairly sharp line separated the *Hippuris/Sparganium* community from the dense stands of the *Equisetum fluviatile* community, but not without some intergradation. The seral stage dominated by *E. fluviatile* occupied water depths of a rather wide lat-

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FIG. 25. South end of Pond 7. Note dense stand of *Equisetum fluviatile* in background; *Hippuris/Sparganium* and *Carex* communities in foreground. (Photo by Shepherd)

FIG. 26. Sharp ecotone between *Carex fluviatile* and *C. aquatilis* communities in Pond 7b, Bremner River. (Photo by Shepherd)

itude, from 6 to 30 inches. The median depth for this community was 18 inches. Many of the taxa characteristic of the deeper water communities still persisted here, but were generally dwarfed and nonreproductive. A dense stand of *Equisetum fluviatile* occupied nearly the entire basin of pond 7 on the Bremner River (Fig. 25).

Succession from the *E. fluviatile* community appeared to diverge into separate seral stages: (1) an anchored mat community dominated by *Equisetum fluviatile*, and (2) a *Carex aquatilis–Carex rostrata–Equisetum fluviatile* reed swamp community that developed into a *Carex aquatilis–Carex rostrata/Potentilla palustris*/moss mat community. The first anchored mat stage was named the *Equisetum fluviatile/Potentilla palustris*/moss community. *Equisetum fluviatile* exhibited a layer or aspect dominance over the *Potentilla palustris*, whereas the mosses formed a carpet of vegetation from which these species emerged. This community was established in water from 12 to 24 inches deep. Most stands were observed to grow at a median depth of 18 inches. Occasionally, *Hippuris vulgaris* and *Sparganium angustifolium* were encountered, occurring as dwarfed specimens. *Utricularia macrorhiza* was found infrequently in scattered clumps. The restricted light conditions of the mat community seem to prevent vigorous growth of these taxa. As organic debris accumulated, the *Equisetum fluviatile* on the mat was replaced by *Carex aquatilis* or *C. rostrata*, thereby forming the final seral stage of the anchored mat community (Fig. 26).

The second seral stage occupied water from 4 to 18 inches deep, with a median depth of 12 inches. *Carex aquatilis* was more frequent in deeper water (6 to 12 inches) intergrading in a narrow ecotone with *Equisetum fluviatile*. Shallow water (4 to 8 inches or less) appeared to restrict the presence of *Equisetum fluviatile* and to promote denser stands of *Carex rostrata*. Many accidents and remnants of low vigor were evident in this community, but only *Eriophorum angustifolium* seemed to assume any importance ecologically. This fact is not evident in the data presented because *Eriophorum* is difficult to segregate from *Carex* without careful examination. Previous field observations of *Eriophorum*

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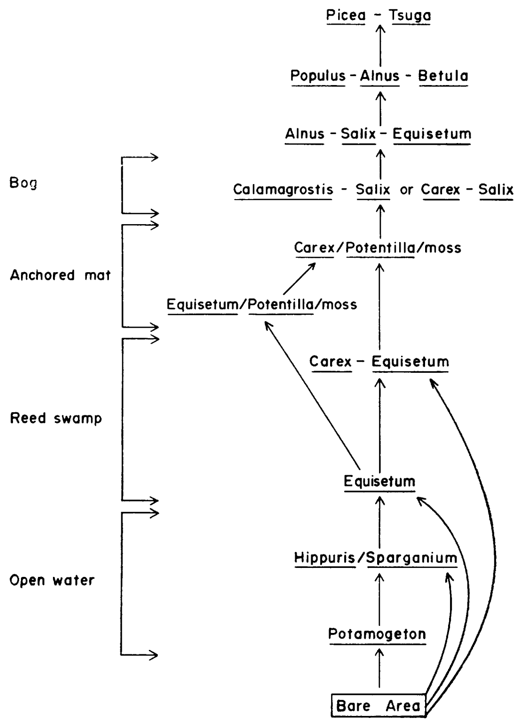

FIG. 27. Diagrammatic representation of the probable anchored mat succession, Bremner River and lower Copper River study areas.

angustifolium, when in the "cotton" stage of development, suggest that this plant is commonly associated with *Carex* stands. *Utricularia macrorhiza* remained reproductive and in good vigor within the *Carex* community and, therefore was considered at least a companion species.

The final seral stage of the anchored mat, the *Carex/Potentilla*/moss community, occurred in wet locations and extended laterally to water as deep as 12 inches, with a median water depth of 6 inches. The same relationship of *Carex aquatilis* to deep water (6 to 12 inches) and *Carex rostrata* to shallow (0 to 3 inches) was as evident in this community as it was in the *Carex* community. However, at this stage of succession other factors became manifest and were apt to restrict plant establishment. Notable among these was an increased acidity and a marked decrease in available nutrients. This was evident in the scarcity of other taxa associated with this community. *Equisetum fluviatile*, a plant of apparently wide ecological amplitude, still persisted on the wetter portions of this mat.

A bog succession consisting of *Carex* spp., *Salix* spp., and moss on very moist locations or *Carex* spp., *Calamagrostis canadensis*, *Salix* spp., and *Equisetum arvense* on drier locations followed the *Carex* anchored mat seral stage. This bog proceeded to an *Alnus/Salix/Equisetum arvense* community as it became drier. Provided the accumulation of plant debris and silt continued, this community was replaced by stands of *Populus tacamahaca*, *P. tricocarpa*, and *Betula papyrifera*. At times these sites were invaded by the climax forest species dominated by *Picea sitchensis* and *Tsuga heterophylla*. However, these species were found infrequently on the flood plains of the Bremner and Lower Copper rivers. The most abundant flood plain vegetation of these areas was *Alnus crispa*.

Anchored mat succession appeared to proceed from any of the first 4 communities, i.e., *Potamogeton*, *Hippuris/Sparganium*, *Equisetum*, or *Carex*. This sere is presented diagrammatically in Fig. 27. Another component of the local hydrosere was the *Glyceria* community. This plant occurred in limited stands over most of the shallow ponds of the study area. Frequently, *Glyceria* was found in nearly pure communities, but as indicated in the plant transect data, it was associated with *Potentilla palustris* and *Carex aquatilis* in some instances.

Nest Location in Relation to Plant Communities and Site Types

The physical and biotic differences in the enclosed water areas of the Lower Copper River are reflected in the variability of the sites available to the trumpeter swan for nesting. Of 40 nests, 21 were in beaver ponds, and nearly 75% of the 40 water basins in this sample had water levels regulated through beaver action. Of these water basins, 32 were less than 35 acres in area (Table 6).

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TABLE 6.—WATER BASINS USED FOR NESTING BY TRUMPETER SWANS IN ALASKA

Type of Water Area	Size in Acres	Nests Number	Percentage
Beaver Impoundment	6– 14	21	51.0
Small Natural Pond	10– 35	8	18.0
Large Lake	40–130	8	23.0
River Scour	10– 35	3	8.0
Total		40	100.0

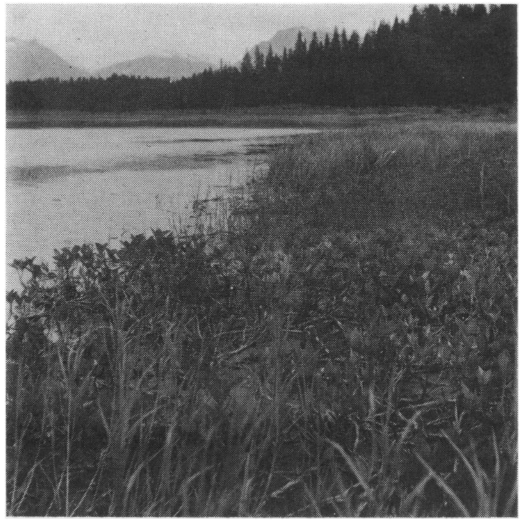

FIG. 28. Heterogeneous stand of vegetation in pond subject to irregular water fluctuations. (Photo by Shepherd)

These data indicate that stable water levels are important factors regulating the establishment and maintenance of uniform plant communities, and that bodies of water from 6 to 35 acres are more likely to support extensive stands of emergent and floating vegetation. The heterogeneous nature of shoreline vegetation in a pond undergoing drastic water level changes is illustrated in the cover map of Pond 7a (Figs. 17 and 28). Generally, ponds or lakes with outlets were able to maintain stable water levels. However, in the case of Pond 7a, extreme annual differences in glacial melt water resulted in the unfavorable water levels.

Erosive wave action and currents in large lakes tended to restrict growth of emergent and mat vegetation, except in protected bays and arms. Large lakes on the study area provided very few nest sites, but were often utilized for feeding, loafing, and molting by nonbreeding swans. Although emergent vegetation was scarce on some of these lakes, dense stands of *Potamogeton* were common. Pondweeds were an important food for molting swans.

Analyses of the nest data indicated a possible affinity toward certain plant communities for nest site location. It was difficult to determine whether the choice was a response to the water depths in which these particular communities grow, or to the vegetation itself. The most realistic analysis seemed to be that both factors were important.

Investigation of 35 trumpeter swan nest sites revealed that 32 (90%) of these nests occurred in 12 to 36 inches of water. Five seral communities occurred within this depth range, including *Menyanthes trifoliata.* The relative importance of these communities for nest sites is presented in Table 7 and graphically shown in Fig. 27.

The fact that 80% of the nest sites were situated in seral communities dominated by *Carex* or *Equisetum* may have been influenced by availability, inasmuch as *Carex* communities were a common constituent of the local hydrosere. However, since the *Menyanthes trifoliata* mat was far more abundant than *Equisetum*, there appeared to be a selective factor involved. Other

TABLE 7.—NEST SITE LOCATION OF TRUMPETER SWANS IN ALASKA

Community	Seral Stage	Nests Number	Nests Total	Percentage
Carex	Anchored mat	7		
	Reed swamp	9	16	47.0
Equisetum	Anchored mat	5		
	Reed swamp	6	11	33.0
Menyanthes	Floating mat	6	6	17.0
Carex–Salix	Bog	1	1	3.0
Total		34	34	100.0

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TABLE 8.—COMPARISON OF PLANT COVER ON 2 SITE TYPES OF NESTING HABITAT OF TRUMPETER SWANS IN ALASKA

Figure Number	Pond		Plant Community Coverage in Acres					Area Covered	
	Type	Number	*Potamogeton*	*Hippuris/Sparganium*	*Equisetum*	*Carex*	*Glyceria*	Total Acres	Percentage
24	Clear Water	4	1.0	1.5	6.0	trace	0.5	8.6	86
19		7	0.3	0.8	9.0	trace	0.5	10.6	76
16	Glacial Water	8	—	—	1.0	trace	0.1	1.2	20
18		9	—	—	—	1.0	—	1.0	11

evidence suggested a strong preference for these communities in the priority listed. This became quite evident during the extensive aerial surveys in 1968 when potential brood lakes could be identified well ahead of the airplane by the type of vegetation.

The most obvious fact was that these genera, especially *Equisetum*, constituted the preferred food species for nesting swans. Secondly, the form of the *Carex* and *Equisetum* communities were similar. Furthermore, this type of physiognomy was similar to the nesting habitat of the trumpeter swan at Red Rock Lakes, which is predominantly a reed swamp consisting of *Carex rostrata*, *Typha latifolia*, and *Scirpus* spp. (Banko 1960).

This leads one to conclude that it is not the *Carex*, *Scirpus*, etc., to which the breeding bird responds, but rather to the physical characteristics of these plant genera and the vegetational community they form. Security seems paramount. The cover afforded by these tall, dense emergents is certainly of more value than the low, spongy floating mat. The less restricting nature of the anchored mat and reed swamp communities allowed swans to move freely, whereas they could only waddle feebly over floating mat.

The few data gathered on plant coverage exemplified the wide range in the quantity and quality of aquatic vegetation from site to site. A comparison of plant cover on glacial and clearwater ponds, both of different origin, clearly showed the limited number of plant communities and restricted vegetation in the glacial ponds (Table 8). However, the fact that swans do nest and can successfully raise broods on such locations suggests that the amount of food, within limits, is not all important in the choice of a nest site. The relationships of pond morphology, cover, and food supply is discussed in greater detail under *Territoriality*.

Zoobiotic Complement

A list was compiled of all animals observed associated with the trumpeter swan habitat in the Lower Copper River Basin (Appendix IV). Although a thorough study of the relationships of these animals to the local ecosystems was neither conducted nor intended, discussion of some species closely affiliated with the ecology of the swan follows under BREEDING BIOLOGY.

BREEDING BIOLOGY

Spring Arrival

Information concerning spring arrival of the trumpeter swan on the south-central Alaska breeding grounds is limited because the coincidental arrival of whistling swans and the free association of the 2 species tends to mask trumpeter swan activities. The earliest spring swan arrivals in the Cordova area, where some fresh water is available nearly all year, are undoubtedly trumpeters. On 27 February 1959, a flock of 50 or more swans was observed by Cordova residents near Hartney Bay. This was an extremely early record and was probably a flock of swans that wintered somewhere

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in Prince William Sound or down the coast toward Cape Suckling or Yakutat. The fact that trumpeter swans tend to winter close to the breeding grounds when open water is available may have survival value for them inasmuch as the cygnets are but poorly developed at best by freeze-up.

Thousands of swans usually arrive by 20 March on the Copper River Delta and remain abundant until late April. Most of these are whistling swans enroute to their breeding grounds along the Bering Sea coast. Pairs were observed loafing on melt-water pools and on frozen lakes along the lower Copper River as late as 8 May 1959 waiting for ponds to thaw sufficiently to allow nest construction. Most of the migrant whistlers had already departed. Despite retarded nesting conditions upstream and at higher elevations, trumpeter swans have often been observed on open water streams in the Gulkana Basin, 160 miles inland at 2,500 ft elevation, by 15 April.

Arrival dates on the Kenai Peninsula are later than those at Cordova. Except for the occasional trumpeter swan wintering in the area, the earliest recorded arrival date was reported by Kenai Refuge personnel, who saw 4 adult and 4 yearling swans at the outlet of Skilak Lake, on 31 March 1959. By mid-April about 15 to 20% of the breeding popluation will have arrived. These are scattered in small groups on ice-free streams or at lake outlets. The Moose River near the Sterling Highway becomes a favorite gathering place as soon as it is open. By 1 May, 150 swans may be seen on the river, coinciding with the departure of swans from the Copper River Delta. They remain at this location on the Moose River until their nesting sites become ice free and then gradually move out. All pairs usually have occupied their nesting territories on the Kenai Peninsula by 20 May.

Pair Formation

Little is known regarding the minimum age at which trumpeter swans pair and nest in the wild. The 1959 Annual Report of the Delta Waterfowl Research Station contains an account of a 4-year-old female pairing and nesting successfully at their station. On the Malheur National Wildlife Refuge in Oregon, Erickson stated that, "The first mated pairs develop during the third year, when they seem to resent intrusion by other single or paired birds . . . One 3-year-old pair, which was separated from the others, made a rather listless attempt at nest construction, but the effort was abandoned before the 'nest' had passed the 'platform' stage. This same pair again attempted nest construction and were seen copulating two years later." This led Banko (1960) to observe, "Whatever the average minimum breeding age of trumpeters may be, the initial age at which a wild pair comes into breeding mood and nests may be influenced somewhat by the quantity of unoccupied territory located in suitable nesting habitat."

This theory has since been supported by the successful nesting of at least 3 pair of trumpeter swans at 33 months of age on the Lacreek National Wildlife Refuge, Martin, South Dakota. During the years 1960–1962, 57 cygnets were transferred from Red Rock Lakes Refuge to Lacreek Refuge. Monnie (1966) carefully documented the breeding behavior and nesting success of these known-age swans. Some of them formed firm pair bonds and established territories by the time they were 20 months of age and 2 pairs nested the following year within these territorial limits. Monnie concluded that "It is possible that the early pair formation and successful nesting of the Lacreek transplanted trumpeters was stimulated by the lack of competition for acceptable nesting habitat."

Minton (1968) banded and studied a population of wild mute swans (*Cygnus olor*) in England intensively from 1961 to 1967. Of 60 known-age swans, 26 nested and laid eggs for the first time at the age of 3 years and another 21 of them at the age of 4 years. Two females, mated with older males, were known to nest at the age of 2 years.

Our intensive ecological study in south-

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central Alaska did not extend long enough after banding a representative sample of cygnets to shed further light on this physiological aspect of trumpeter swan behavior. Circumstantial evidence indicates that a lack of habitat in Alaska has had little, if any, inhibitory influence on the breeding success of trumpeter swans at the earliest possible age.

Mating fidelity in trumpeter swans is another little-known facet of their life history. Permanent mating bonds may be kept intact as long as both members of the pair live. The fact that the loss of one member of a pair will not keep the survivor from remating was verified during the course of this study. A marked female of undetermined age remated with another swan of undetermined age the year following the loss of her mate. Minton (1968) reported about 85% of breeding pairs of mute swans stayed together from one year to the next, but that, during a long swan lifetime, deaths, separations, or other circumstances were apt to cause mate changes.

Territoriality Among Breeding Swans

Size of Territory

Territorial size is largely governed by the size of each water basin. These basins consisted of individual units ranging form 6 to 128 acres. Only in 4 known instances were there more than one pair nesting on a single body of water. On the Copper River this was on Peninsula Lake (Fig. 2), which is over 1,600 acres in size. The nest sites on this particular lake were in an extensive marshy area of approximately 450 acres, with about 150 acres of uninterrupted emergent vegetation per pair. A lake on the Kenai supported 2 nest sites nearly a mile apart, and no intraspecific defense of either was observed. Martin Lake on the Copper Delta had 3 broods, and 4 broods were observed on a beach scar lake near Yakataga. Each of these latter 2 lakes are approximately 4 miles long and heavily vegetated.

On contiguous nesting areas at Red Rock Lakes, territories averaged from 70 to 150 acres of marsh per nesting pair (Banko 1960). There appeared to be a relationship in these areas between the morphology of the shorelines and the number of territorial pairs. The D_L of the 500-acre Swan Lake, which supported one pair of swans per 70 acres, was over 4.0, or very irregular. Lower Red Rock Lake had a D_L of about 3.0 and covered 1,500 acres. Although this lake had a longer, more regular shoreline, it supported only 1 pair per 150 acres. Data from the Copper River area indicated that the amount of food available and area per nesting site both varied considerably, suggesting that territorial isolation was more important than either food supply or size of area.

The square root of the distance between individual nests plotted against frequency, gives a frequency polygon. The shape of this polygon indicates the distribution pattern. A symmetrical polygon indicates random distribution; a polygon skewed to the left indicates a clumped distribution (Dice 1952). Analysis of the Red Rock Lakes data shows a polygon skewed to the right suggesting a uniform distribution. Odum (1959) stated that a uniform distribution may occur where competition between individuals is severe or where there is positive antagonism which promotes even spacing. These data suggest that special requirements in the swan are strict and that territorial behavior is developed to a high degree.

Territorial Maintenance

Observations of swans in the Copper River area indicated that territorial maintenance continued from the time the pair arrived on the nest site until well into the brood season. Only occasionally were alien swans seen on an established territory, and these were always paired or single swans without young. After the eggs hatched and the wing molt began, aggressive behavior appeared to wane, but often returned as the adult swans became newly fledged.

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Defense of Territory

Territories appeared to be appropriated as soon as the paired adults could find open water on the nesting ponds. Pairs were occasionally noted to occupy frozen ponds. No observations of intraspecific defense were made this early in the season. On one occasion following the ice breakup a pair defended its territory vigorously against the inadvertent intrusion of another pair which was frightened from their own nesting area by a human trespasser. The pair on the usurped territory approached the intruders with extended necks and arched wings, while at the same time violently treading the water. This physical action was accompanied by a staccato trumpeting on the part of the defending swan. After a few preliminary rushes from the defenders, the trespassers quickly left the area. There were no opportunities to observe defense against deliberate aggression where one pair of swans tried to take over another's territory. This probably was because enough nesting sites were available so there was no need for crowding, and newly formed pairs could pioneer into new territory easily.

Tolerance toward other species of birds, including waterfowl, was quite apparent. In one instance a trumpeter swan, Arctic tern (*Sterna paradisaea*), and common loon (*Gavia immer*) nested within a radius of 30 ft. It was not uncommon to see ducks and other small birds loafing on swan nests. On the other hand, most mammals were not tolerated near a nest. A beaver was once observed idly swimming toward an occupied nest. As he approached, the larger of the 2 swans immediately charged. This swan arched its neck, spread its wings, and began to tread on the beaver with its feet. Because the water was shallow, the beaver could not dive and, consequently received an extensive beating from the swan's wings, bill, and feet. The beaver was pursued to a point about 100 yards from the nest. At this point the chase was discontinued and the swan returned toward the nest flexing its wings and bobbing its head. Another time, a cow moose (*Alces alces*) was observed under attack on the Kenai. The moose was swimming across a small body of water toward a point of land where a swan nest was located. As the moose approached the point, the swan rose from her nest and violently flapped the hind quarters of the moose. Needless to say, the startled cow beat a hasty and undignified retreat.

Aggressive display toward airplanes was frequent. This action usually occurred as the airplane flew low over the nest. Often, one or both of the swans would stand on the nest, arch their wings and extend their necks (see Frontispiece). Once the largest adult of a pair came within 10 ft of a float plane that was drifting toward a nest site on a lake near the Bremner River. This bird exhibited the characteristic arched wings and extended neck posture. It also hissed continuously and did not depart until the engine of the airplane was started and accelerated. In another instance, on the Kenai, a swan rose from her nest, flew directly into the wing of a float plane taxiing toward her, and ripped the aircraft fabric with her bill. The impact knocked her to the water, where she appeared stunned for a moment before taking to the air and departing. The pilot had attempted to steer the plane out of her path but she deliberately maneuvered to hit the plane, so there was no doubt as to her intent.

In no instance on the Copper and Bremner river study areas did nesting swans show any aggressiveness toward humans. In fact, they were exceedingly wary at the approach of man and vacated their nests immediately. In each instance when agressiveness toward the plane was shown, the swan departed as soon as the pilot stepped from his craft. The same wariness was displayed when swans were approached by boat or canoe. As soon as the occupant of the boat was identified as a human, the swans quietly slipped off into the concealing vegetation. With broods, their concealment was even quicker and more effective. As long as an observer did not depart from

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his enclosed vehicle and maintained a respectable distance, nesting swans remained normally alert but were not greatly alarmed otherwise. Repeated observations of a pair of nesting swans for the duration of their incubation were made from a parked truck at a distance of 250 yards on the Copper River Highway. These swans did not leave the nest site as long as the observer remained in the vehicle.

Once on the Kenai, however, Troyer was attacked on the ground by a nesting swan and retreated hastily before bodily contact was actually made.

Nesting

Nest Location

Nearly all the trumpeter swan nest sites found in south-central Alaska were placed in emergent vegetation. Nests were constructed by the swans from nearby marsh vegetation. The average water depth surrounding 32 nests was 21 inches, with a range of 12 to 36 inches. In the process of building the nests the bottom of the pond surrounding the nest was deepened slightly. Therefore, in determining the range in depth in relation to plant communities for all nest sites, measurements were taken at the edge of the undisturbed plants.

At variance with conditions at the Red Rock Lakes Refuge (Banko 1960) no nests were found on muskrat houses, possibly because this type of dwelling is rarely used by muskrats in Alaska. Frequently, small feed platforms or "push-ups" are built by the muskrat, but there is no indication that these are used by swans, possibly because they are so small. One nest was discovered on an abandoned beaver house. Occasionally, water receded from a nest after it had been built in a marshy situation, leaving it as much as 100 yards from the edge of the permanent shoreline at the time of hatching. The major exception to over-water nest sites occurred on the Kenai, particularly on lakes closely surrounded by timber. Under these circumstances nests were sometimes located on small islands well away from the shoreline (Fig. 29).

Nest and Nest Site Occupancy

Nests were often renovated and reused from year to year. An index to nest site occupancy can be calculated by dividing the number of times a pair of swans occupied a nesting territory by the total years these sites were observed. Nest site occupancy on the Bremner and Copper river study areas during 1957 through 1959 was 63%. During the same period on the Kenai Peninsula, nest site occupancy was 88%. During the next 8-year period, 1960 through 1967, nest site occupancy on the Kenai dropped to 73% (Table 9).

The differences between these areas and between periods of time on the Kenai may have been due to disturbance factors. Since all the Kenai swan investigations were accomplished by aerial surveys and little ground reconnaissance was attempted during the first 3 years, while intensive ground studies were conducted on the Bremner study area, the lower occupancy index on the latter may have been a reflection of disturbance by the investigators. Five new nest sites were occupied on the Kenai in 1959 without an increase in nesting pairs. The movement of swans, establishing new territory and abandoning old, in this and subsequent years, was attributed by refuge personnel to disturbance created by intensive helicopter and seismic activity during oil explorations.

On the Bremner River study area where 13 pairs of swans nested successfully in 1957, there were only 6 in 1958, and 2 of these were on new territories. In 1959, 10 pairs nested on the Bremner area, but 2 of these pairs also selected new sites. The other 8 repaired and used previously occupied nest structures. The instability in this population was probably brought about by intensive activity on the breeding marshes, including the repeated capture and handling of both cygnets and molting adults. Recapture of banded adults con-

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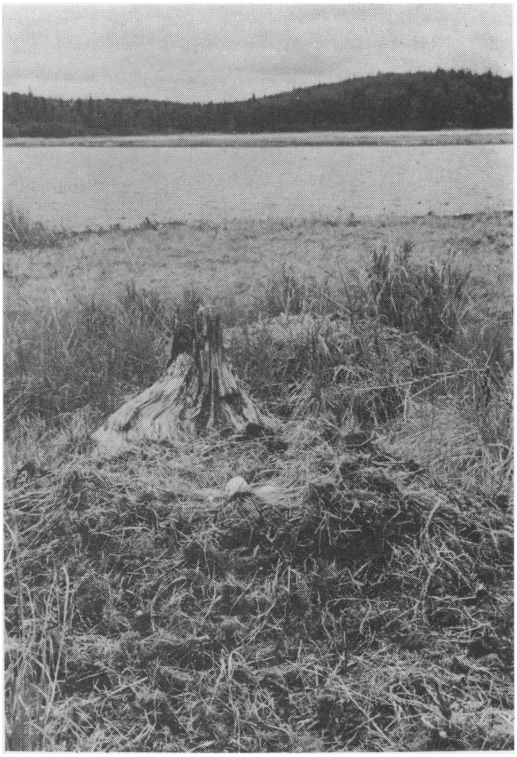

FIG. 29. Trumpeter swan nest on an island in Elephant Lake, Kenai National Moose Range. This atypical island site had been occupied consistently during 10 years of observation. Note eggs in current year's nest and previous year's nest in background behind stump. (Photo by Troyer)

firmed that pairs will return to a previous year's nest, and that disturbance will cause desertion of a nest site and movement to a new area. For example, 2 adult males, both banded on 4 August 1958, were recaptured at the same respective nest sites, one on 27 June and the other on 27 July 1959. An adult female was banded at Pond No. 1 (Fig. 2) on 13 August 1957. The next summer at a new nest site on Pond No. 8, a male was caught and banded but his mate was not. At this same site on Pond No. 8 on 5 August 1969, an adult female and one cygnet was captured but her mate was not. The female was the same one banded on Pond No. 1 in 1957.

TABLE 9.—TRUMPETER SWAN NEST SITE OCCUPANCY, ALASKA

	Bremner/Copper Study Areas 1957–1959		Kenai Study Area 1957–1959		Kenai Study Area 1960–1967	
Site No.	No. years site observed	No. years site used	No. years site observed	No. years site used	No. years site observed	No. years site used
1	3	2	1	1	8	6
2	3	1	0	—	8	7
3	3	1	0	—	4	4
4	2	2	3	3	8	6
5	3	2	3	3	8	7
6	3	1	1	1	8	5
7	3	2	2	1	8	5
8	3	3	3	2	8	6
9	2	2	3	3	8	5
10	3	1	2	2	8	6
11	3	3	3	3	8	7
12	3	3	0	—	7	6
13	3	1	0	—	7	6
14	3	1	3	3	8	6
15	3	2	1	1	8	7
16	3	3	0	—	7	7
17	3	1	3	2	8	3
18	3	2	3	3	8	3
19	—	—	3	3	8	6
20	—	—	0	—	8	5
21	—	—	3	3	8	7
22	—	—	2	2	8	5
23	—	—	3	2	8	7
24	—	—	0	—	8	5
25	—	—	1	1	8	6
26	—	—	3	2	8	7
27	—	—	2	1	8	5
28	—	—	3	3	8	5
29	—	—	1	1	8	5
30	—	—	0	—	5	4
Total	52	33	52	46	230	169
	Occupancy Index 33/52 = 63%		Occupancy Index 46/52 = 88%		Occupancy Index 169/230 = 73%	

Nest Construction

Both the male and female swans were active in construction of the nest. Time needed for construction depended on whether the nest was to be newly developed from the ground up or merely repaired. A pair was observed to spend 2 weeks completing the construction of a new nest on the Copper River Delta. However, the first egg was laid only 6 days after the nest was begun.

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FIG. 30. Shoreline trumpeter swan nest in *Carex* community. Rifle on nest is 44 inches long. (Photo by Shepherd)

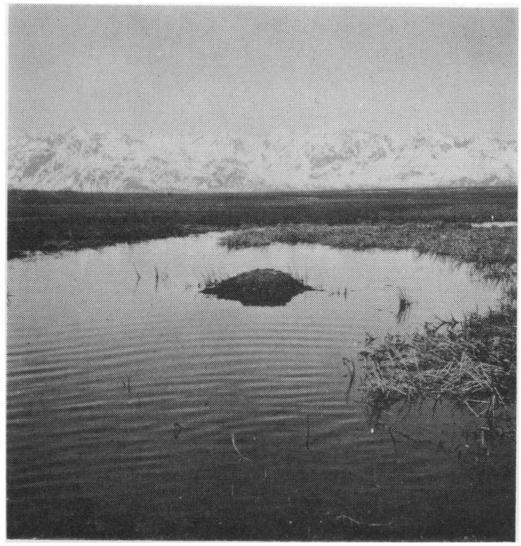

FIG. 31. Ground view of "moat" surrounding trumpeter swan nest in *Carex rostrata* community. (Photo by Shepherd)

The nest was usually built from 10 to 600 ft from the shore, depending upon cover and water depth. Occasionally one was located on or near the shoreline of a small islet in a large lake. The nest consisted of a cone-shaped mound of rhizomes and stems of *Carex*, *Equisetum*, and *Potentilla*, from 6 to 12 ft in diameter (Fig. 30). Some mounds reached as much as 36 inches in height, although 36 nests had a mean height of only 18 inches. As the swans pulled and rooted nest materials from the bottom, they formed a "moat" around the nest. This open area was measured up to 32 ft in diameter, but the average of 19 "moats" was 25 ft. The open area increased in size with each year's use inasmuch as vegetative scars, aquatic as well as terrestrial, heal slowly in the sub-Arctic regions (Figs. 11 and 31).

The nest cavity varied from 10 to 16 inches in diameter and from 4 to 8 inches in depth. Little down was added to this depression even as incubation progressed. However, a soft covering of finely shredded plant material and mosses was used to conceal the eggs when the parents were absent.

The final construction of the nest probably was accomplished by the pen, whereas the cob confined himself to obtaining nest materials. After the initial mound was rather quickly formed, the finishing of the nest was done at a leisurely pace. Generally the pen remained on the nest (if egg laying had begun) and reached out with her bill to receive "clods" of vegetation transported to the nest by the cob. The cob uprooted nest materials with short, jerking motions of his head and neck, moving the material toward the nest with a series of tosses. These clods of vegetation were then placed at the base of the nest where the pen could reach them.

Occasionally the pen stood up in the nest and added bits of material to it or turned the eggs with her bill. The pen rarely sat on the eggs for more than 15 min at this time and did not sit continually until the clutch was completed.

The nest served as a loafing platform for the entire family after the eggs hatched. Nest sanitation was not practiced and fecal

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TABLE 10.—CLUTCH SIZE OF TRUMPETER SWAN NESTS IN THE COPPER RIVER VALLEY AND ON THE KENAI PENINSULA, 1958–1969

Clutch Size	Number of Nests								
	Copper River Valley			Kenai Peninsula					
	1958	1959	1968	1964	1965	1966	1967	1968	1969
1			1		1				
2		2		2		1			
3		2	3	3	2	2	2	1	
4	3	6		2	2	6	5	6	2
5	2	9	9	11	9	10	6	8	13
6		4	7	2	11	11	7	6	5
7	1	1	3		8	2	4	2	4
8					1		1		1
9					1				
Total Nests	6	24	23	20	35	32	25	23	25
Mean Clutch Size	4.9	4.6	5.2	4.4	5.7	5.1	5.4	5.0	5.6

matter was deposited freely over the trampled mound. Old abandoned nests were also utilized as resting sites by broods and adults.

Egg Laying

From 1 to 7 eggs were laid at approximately 2-day intervals on the Copper River study areas where the mean clutch size for 53 complete sets of eggs was 4.9. From 1 to 9 eggs were laid on the Kenai where the mean size of 160 completed clutches was 5.3 eggs (Table 10). These figures compare with a mean of 5.1 eggs in 74 clutches on the Red Rock Lakes Refuge (Banko 1960).

The mean clutch size in Alaska varied from a low of 4.4 (in 1964) to a high of 5.7 (in 1965). It is interesting to note that whistling swans on the Yukon–Kuskokwim Delta reacted to the very late spring of 1964 with the smallest clutches recorded. The average size of 41 clutches in 1964 was 3.3 eggs compared to 5.0 eggs for 42 nests in 1967, an early season (Lensink 1968). Smaller clutches in late seasons would tend to speed up the whole reproductive process and give the smaller brood a better chance to mature enough to migrate in the fall or otherwise cope with the onset of winter. For instance, the hatching (and fledging) date would be advanced 2 days for each reduction of 1 egg in clutch size. Thus, cygnets from a 1- to 2-egg clutch would be on the wing approximately 2 weeks earlier than birds from a 7- to 8-egg clutch, other things being equal. This would be a significant factor in survival for a species where a few days delay in the spring or advance in the fall count under normal circumstances.

Alaska trumpeter swan eggs are noticeably larger than those of the Red Rock Lakes swan. The mean length and width of 146 eggs from south-central Alaska was 117.4 mm (± 8.8 mm) by 75.0 (± 1.0 mm). These eggs ranged from 109.8 mm to 125.0 mm in length and from 69.8 mm to 81.0 mm width (Appendix II). In comparison, the mean length and width of 109 eggs checked at the Red Rock Lakes Refuge was 110.9 mm by 72.4 mm, ranging in length from 104 mm to 124 mm and in width from 69 mm to 74 mm (Banko 1960).

Incubation

The incubation span for trumpeter swan in Alaska was consistent with that reported elsewhere. Banko (1960) gave a normal incubation period of 33 to 37 days for swans at the Red Rock Lakes Refuge. A nest of trumpeter swan eggs at the Delta

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Waterfowl Research Station in Manitoba hatched in 36 days (1959 Annual Report), whereas Delacour (1954) listed an incubation period of 36 to 40 days.

On the Kenai Peninsula the incubation period varied from 33 to 37 days. A detailed record of 6 nests on the Copper River showed an incubation period ranging from 33 to 35 days. In the latter area there was no indication that the cob assisted in incubation at any of these nest sites. A nest on Pollard's Lake near Kasilof (Kenai Peninsula) was within view of the Fletcher home where Mr. and Mrs. Fletcher spent considerable time observing swan activity. They reported that both male and female frequently left the nest site together to feed and, perhaps, relax. We noted the absence of both swans simultaneously at other nest sites as well during incubation.

Three specific observations in 1966 on the Kenai illustrate the degree of fidelity swans show toward their nesting site at various stages of incubation:

Nest number 3.—On 10 June at 11:30 AM, one week prior to hatching, both swans were absent from the nest and located on a small lake a mile north of the nest site. When checked again at 2:00 PM both swans were at the nest site with one incubating. The eggs had been covered during their absence.

Nest number 7.—On 3 June at 10:00 AM, both swans were absent from the nest site. The eggs were covered and both swans were on an adjoining lake 0.25 mile distant. When checked again in late evening of the same day, they were back at the nest and one was incubating. The following day at 9:30 AM, the pair was again off together, but nearby. The eggs were covered.

Nest number 10.—This site was easily visible from the Swan Lake Road and the pair was subjected to considerable disturbance. On 15 June, after they had incubated for approximately 24 days, a check revealed that only 3 of the original 5 eggs remained. Shell fragments on the ground nearby indicated that the loss was caused by predation, whether or not during the swans' absence could not be determined.

On 21 June, a party fished on the lake and then camped on an island adjacent to the nest site. The swans remained off the nest most of that day and left the eggs uncovered. Inasmuch as these swans had been disturbed for a good portion of another day earlier in incubation, it was assumed that the nest would be abandoned at this time. The next day, however, they were again incubating and all 3 of the remaining eggs hatched on 26 June.

These observations indicate that swans leave nests unattended for varying periods of time during incubation and that, in some instances, absence from the nest for several hours may not have a detrimental effect. Presumably the further along a pair of swans carries incubation, the firmer their nesting bond becomes. Most desertion accurately documented on the Copper River study areas occurred during the egg laying period or early in incubation. Furthermore, when an embryo has developed almost to maturity, it can maintain viability without incubation for a much longer time than it can early in its development. This was demonstrated and documented in the following study during the early stages of this trumpeter swan project.

During storm-driven flood tides on the Copper River Delta in 1959, waterfowl nests in various stages of incubation were subjected to flooding in sea water of less than 50 F. Despite the prolonged temperature stress to which eggs were subjected, a hatching success of 83.5% of 1,017 Canada goose eggs attests to the hardiness of these large birds. Ducks of several species were almost as successful. Of 850 eggs under observation in 132 duck nests, hatching success was 80.4% although many of

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TABLE 11.—ESTIMATED NESTING CHRONOLOGY FOR TRUMPETER SWANS[1]

Year	Estimated Date				Extent of Hatch (first to last nest)
	First Nest Begun	First Egg	Incu-bation Started	First Nest Hatched	
1957	5 May	11 May	25 May	29 June	28 days
1958	22 April	28 April	12 May	16 June	34 days
1959	27 April	5 May	19 May	23 June	29 days

[1] This estimate is based on a 14-day nest-building and egg-laying period, 35-day incubation period, and brood ages.

the dabbling duck nests escaped the prolonged submersion of goose nests (Hansen 1961).

The large volume of a trumpeter swan egg in relation to its surface area would tend to minmize heat loss so that an incubating swan could be absent from the nest a longer time than birds with proportionately smaller eggs under similar circumstances.

Hatching Success

Copper River Study Areas

The estimated nesting chronology on the lower Copper River indicated that nesting and incubation began as early as the third week in April and extended through the first week of July. Brood observations showed a 14-day spread in mean hatching dates for the 3 years on the study area. This difference was attributed to annual variations in date of spring "break-up." Late springs tended to retard nesting and hatching whereas early springs accelerated these processes. The hatching period was comparatively short, ranging from a low of 28 days in 1957 to a high of 34 days in 1958, or roughly one month (Table 11).

During 1959 on the lower Copper River, 38 nests were under observation. Of this number, 29 (76%) were incubated successfully with one or more cygnets. The number of cygnets per brood at hatching varied slightly from one year to another. A 55% hatching success of 179 eggs in these 38 nests included egg loss by predation and abandonment, infertile eggs, and dead embryos. In comparison, there was a hatching success of 76% of the eggs in the 29 successful nests (Table 12).

Of the 179 eggs, 22 could not be accounted for after hatching. They may have been lost to predators or hatched and escaped as unobserved cygnets. Because the nests were under close observation during the hatching period, there was slight chance that these eggs were accidentally buried in the debris and missed. Exposed eggs were observed in hatched nests for more than a month after incubation was terminated. A more likely explanation is that the missing eggs hatched and the cygnets either succumbed very soon after hatching or were able to hide exceptionally well from the outset.

Destruction of 4 trumpeter swan nests was attributed to mammalian predation. Three of these nests apparently were destroyed by bears, as indicated by bear tracks and dung about the nest. Eggs taken by bears were always eaten entirely, and

TABLE 12.—FATE OF 38 TRUMPETER SWAN CLUTCHES, LOWER COPPER RIVER, ALASKA[1]

	Hatched	Destroyed	Abandoned	Remaining in Nest[2]	Unaccounted For	Total Eggs Laid
Bremner River	21	10	10	1	4	46
Copper River Delta	20	5	0	8	5	38
Martin River	58	9	4	11	13	95
Total	99 (55.3)[3]	24 (13.4)	14 (7.8)	20 (11.2)	22 (12.3)	179

[1] Twenty-nine of these nests hatched successfully, with one or more eggs hatching (76%).
[2] Included 6 addled, 4 infertile, and 10 feathered embryos.
[3] Percentage of total eggs laid.

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TABLE 13.—COMPARISON OF HATCHING SUCCESS OF TRUMPETER SWANS IN ALASKA BY AREAS, 1959

Census Method	Area	Hatched		Destroyed or abandoned		Remaining or other		Total	Chi-square
		Obs.[1]	Exp.[2]	Obs.	Exp.	Obs.	Exp.		
Ground	Bremner River	21	25.4	20	9.8	5	10.8	46	16.677[3]
Air + ground	Copper Delta	20	21.0	5	8.1	13	8.9	38	3.121
Air + ground	Martin River	58	52.5	13	20.1	24	22.3	95	3.212
Total		99		38		42		179	23.010

[1] Observed.
[2] Expected.
[3] Significant at the 5% level.

only a few fragments of shell remained in the nest. Both brown bears (*Ursus* sp.) and black bears (*Euarctos americanus*) were common on the study area.

A nest of 5 nearly hatched eggs on the Bremner River was destroyed by a wolverine (*Gulo luscus*). Tooth marks on the eggs and tracks were instrumental in aiding identification of this large mustelid. The 2 eggs which remained in the nest were bitten in half longitudinally and the contents removed. All nests destroyed by predators were situated in vulnerable sites close to the shoreline.

High water was responsible for destruction of one nest on the Bremner River. Nest desertion was restricted to 3 nests. The causes of these desertions were unknown, but 2 occurred on the Bremner River where there was considerable human activity.

Only 4 of the 20 eggs remaining in nests had intact yolks. Six other eggs were addled and 10 contained downy embryos. It was common to find more than 1 unhatched egg in a nest. Often, at least 2 were left. Fully developed embryos were found commonly in the eggs which remained after hatching, at least more frequently than addled eggs.

Statistical analysis of the difference in success between the 3 Copper River study areas showed a difference in hatching success between those areas censused by ground and those by air and ground (Table 13).

TABLE 14.—FATE OF TRUMPETER SWAN CLUTCHES ON KENAI PENINSULA, 1965–1967

	1965	1966	1967	Total
Nests hatched	31	21	21	83
Nests abandoned or destroyed before hatching	5	5	7	17
Percent of nests hatched	86.0	85.0	60.0	79.0
Total eggs in successful clutches	184	151	115	450
Eggs hatched in successful clutches	158	129	84	371
Percent of eggs hatched	85.0	85.0	73.0	82.4

Kenai Peninsula Study Areas

Nesting chronology on the Kenai was essentially the same as on the lower Copper River except each phase was initiated an average of about one week later. Thus, the earliest incubation was recorded to begin on 1 May, and the earliest hatching on 4 June continuing through the first week of July. In 1965, the recorded hatching span of 15 nests extended from 12 June through 20 June. In 1967, the span of 8 nests was from 7 June through 3 July.

Nesting in general, and percentage of eggs hatched in successful nests, was consistently higher on the Kenai. During the years 1965–1967 a special effort was made to obtain hatching data from as many nests as possible. The number of successfully hatched nests ranged from a high of 88% in 1965 down to 60% in 1967, with an average of 79%. The hatching success of eggs from clutches successfully incubated ranged

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from 85% in 1965 and 1966 down to 73% in 1967, with an average of 82% (Table 14).

It was interesting to note that pairs of swans at certain locations were consistently successful nesters year after year. At other sites pairs of swans were consistently poor nesters, bringing off only partial clutches or failing entirely. Assuming that the same pair of swans returned and successfully claimed its own territory each year, what would account for this obvious difference in reproductive success of individuals? Are some birds naturally less adept and assiduous than others of their species, even in the basic function of reproduction? Or are the less successful birds wedded to marginal habitat where none could do better? Except where human activity has been allowed to intrude and create an obvious deterrent, the less successful sites appear no different, superficially at least, than the better ones.

Cygnets

Brooding and Parental Care

Observations during the final stages of incubation indicated that the average clutch required about 24 hr to hatch. A hatching interval (time between hatching of first and last egg in the same clutch) of only 6 hr was recorded for one nest. The first cygnet that hatched from this nest weighed 225 g (7.95 oz) at 12 hr, whereas a still damp brood mate of 6 hr weighed 210 g (7.41 oz). In keeping with the noticeably larger eggs of Alaska trumpeter swans, these cygnets are larger than 2 cited by Banko (1960), 7.5 and 7 oz, respectively.

The female (distinguishable from the male which had been previously marked) was known to have brooded these young at least 48 hr. Cygnets are usually brooded for 24 hr, and even longer if the weather is inclement. An example of extended brooding was recorded on the Bremner River study area. Here a female (male marked) was seen during mid-afternoon of a cloudy, cool day on a nest which she had been continuously incubating for the previous 2 days or more. She appeared to be asleep, with her head tucked under a wing, but left the nest when the investigator approached to within 100 ft. Immediately, the young tumbled out and proceeded to follow the female. They were caught and, from their size, were judged to be at least 3 days old. Brooding may also take place on the open water where the cygnets are covered by the adult's wings.

The parents appeared constantly attentive toward the young, and the family performed its daily activities in a closely-knit group. If slowly or unobtrusively disturbed by humans, the young usually were led away by one or both of the adults. In a normal sequence, the adult capable of flight would swim away as if to decoy the intruders while the flightless adult led the young to cover and then departed. On one occasion when a brood was separated from its parents by the investigators, a mew gull (*Larus canus*) immediately started to harass the cygnets. This was simulated as well by our observations from a low-flying aircraft which invariably caused a family group to gather tightly usually with the cygnets between the parents. When the young were very small the family tried to seek the shelter of emergent vegetation under these circumstances, but later on they frequently remained tightly grouped in open water. The consistency of this behavioral pattern indicates that the close surveillance given the young by their parents allows little opportunity for attack by aerial predators.

On the Copper River study areas the parents became less protective in their care as cygnets neared flight stage. In late August and early September it was common to see only one adult with the brood and on a few occasions both adults were missing for extended periods up to several days, although they always returned. During the aerial survey in 1968, on the other hand, only 2 broods of 257 were observed

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TABLE 15.—COMPARISON OF CYGNET SURVIVAL LOWER COPPER RIVER STUDY AREAS

Method of Disturbance	Area	Survival		Mortality		Total	Chi-square
		Obs.	Exp.	Obs.	Exp.		
Air	Martin River	40	38.0	5	7.0	45	0.676
Air and ground	Bremner River	20	17.8	1	3.2	21	1.784
Air, ground, & other	Copper River	11	15.2	7	2.8	8	7.460[1]
Total		71	71	13	13	84	9.820[1]

[1]Significant at the 5% level.

without parents and only 10 broods with but a single parent. Thus, parental fidelity to the family appears very strong.

Disturbance Factors in Relation to Preflight Movement and Mortality

The Copper River study led to the conclusion that disturbance by humans during the brood season should be kept at a minimum. A statistical comparison of the 3 individual study areas that were subjected to various types and amounts of disturbance showed a significant difference in cygnet mortality on the Copper Delta (Table 15).

Access to both the Martin and Bremner rivers by the public was extremely difficult and, thus, was minimal or nonexistent except for the investigators. The Copper Delta study area, on the other hand, was accessible for its entire length by a 20-mile public road leading out of Cordova. Several tidal sloughs navigable by small boat dissected the delta from the road seaward. Both commercial and sports fishermen were frequent visitors as well as many people who traveled the road for a casual drive, photography, hiking, picnicking, hunting, target shooting, and other recreational activities. Although the swans on the Copper Delta may not have been molested intentionally by the public, the varied and more frequent level of human activity seems to have had a detrimental effect in comparison to the more isolated nesting areas.

A forced and rapid movement of cygnets from one body of water to another less secure, induced by human intrusion, appeared to be the greatest factor leading to higher mortality rates. An exodus of broods from natal ponds was common when these areas were entered. At times, cygnets were led overland at a rapid pace up to a distance of a mile. Some swans portaged from quiet ponds into the nearby Bremner or Copper River and traveled 2 or 3 miles downstream in currents which ranged from 4 to 8 miles per hour. In one case, a complete brood disappeared after an extended movement. In other instances at least one member of a brood was missing after being forced from the natal marsh. These losses occurred most often in broods with cygnets less than 2 weeks old. It probably would be difficult for a family to establish a suitable new territory under these conditions because it would find good territories already occupied and defended.

Cygnet mortality within the first 8 weeks ranged annually from 15 to 20% of the number hatched. No specific instance of predation was observed nor the immediate cause determined, but most occurred within the first month, and practically none after about 8 weeks. Potential predators were present over the entire swan habitat. Sign of both brown and black bears was numerous around nesting sites. Occasionally, wolverine, wolf (*Canis lupus*), coyote (*Canis latrans*), and otter (*Lutra canadensis*) tracks were noted. Mink (*Mustela vison*) were abundant also. Although potential mammalian predators were active throughout the area, avian predators would undoubtedly have been more effective in picking off small, stray cygnets. Bald eagles were plentiful as far inland as the

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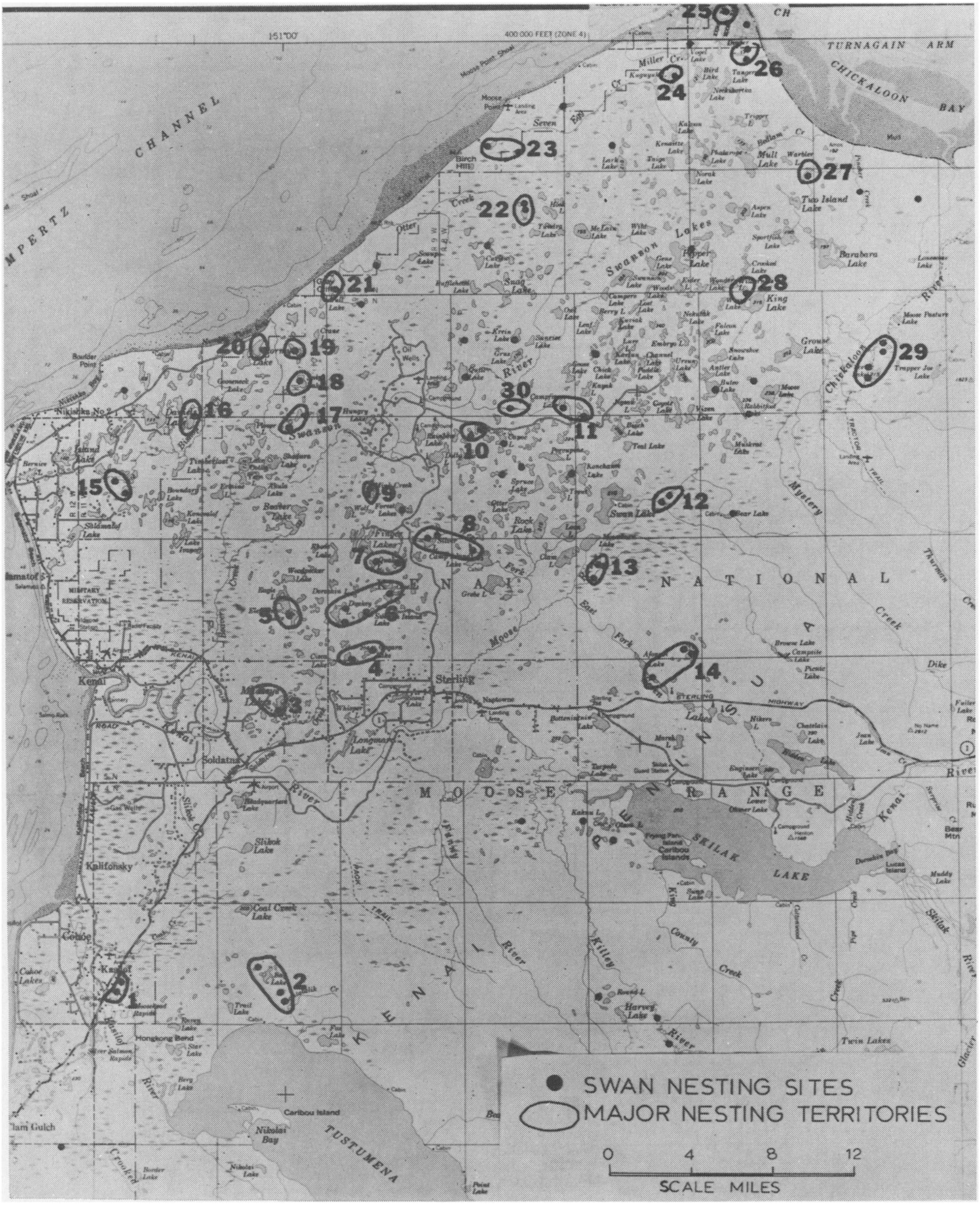

FIG. 32. Trumpeter swan nesting territories and nest sites on the Kenai National Moose Range, 1965–1967.

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Bremner River, nesting in close proximity to swans. Although readily available spawning salmon were a buffer which favored the swan, bald eagles have been observed to take healthy ducks with apparent ease on the coastal marshes of Alaska where they comprise an important portion of the diet at certain times (Imler 1941). Peregrine falcons (*Falco perigrinus*) were also observed in the area as was the efficiently foraging glaucous gull (*Larus hyperboreus*). The extent to which glaucous gulls prey on waterfowl, when broods are scattered or driven into marginal security situations during banding activity and other studies, has been well documented on the Yukon Delta (Olson 1951).

The apparent man-induced preflight movement of broods on the Copper River, despite the mortality associated with it, was no greater, and in some years less, than that observed in a subsequent brood study on the Kenai which was conducted entirely from the air. Preflight movements of various broods were recorded in 1965, 1966, and 1967 to gain an insight into the territory occupied during this period, as well as other behavioral characteristics and mortality rates. This was accomplished by aerial observations, and the location of broods was plotted on 1:63,560 scale maps (Fig. 32). An attempt was made to check each brood every 3 days but on some occasions a week elapsed between checks. At times a brood could not be located until more extensive time lapses occurred.

Brood movements from nest Sites 3, 7, and 9 were recorded all 3 years. Broods from Sites 5 and 6 were recorded 2 different years, and from Sites 8, 10, and 30 in 1966 only. Movements varied considerably. Some broods, such as Nos. 4, 5, 8, and 9, rarely if ever ranged outside the lake on which the nest site was located, while others moved extensively. Usually the route of travel when moving between lakes was through marshy habitat, but on several occasions broods traveled through heavy forests.

There appeared to be a similar pattern of movement of the same nesting pair from year to year, as long as they occupied the same site. When the nest site was changed, the area of movement also changed. Some broods crossed forest areas or swamps numerous times. In 1965, the following observations were made of a brood at Site 3. (Fig. 33).

Seven cygnets hatched on 12 June. When 6 days old, they moved overland to another large lake west of the nest site. On 24 June, at 12 days of age, they were seen moving back to their natal marsh. They remained there until 9 July when they again moved to the large lake to the west, but returned the very next day to the lake containing their nest site. During the next 2 weeks they frequently moved to a small beaver pond 1.5 miles northwest of the nest site. They remained in this general vicinity, moving between various smaller lakes, until they were on the wing.

In 1966, the pattern of this pair was the same (Fig. 34). Twice they were seen traveling through a black spruce (*Picea mariana*) forest between lakes. In 1967, the nest site was changed to the small beaver pond (Fig. 35). That year the movements ranged between the beaver pond and Soldotna Creek Lake, some 2.5 miles distant and slightly north of the 1965 and 1966 range.

The brood at Site 7 moved quite extensively with a similar pattern each year. Once this brood had moved to the Finger Lakes, however, they never returned to the lake on which their original nest site was located. In 1965, when the cygnets were only 6 days old, the parents moved them from the nest site to the northern part of the Finger Lakes in less than 2 days. It was necessary for them to cross dense forests to negotiate the route.

In 1966, the brood from Site 10 appeared at the south edge of its natal lake 2 days after hatching. This observation was made at 7:30 AM. At 9:30 PM they were located on a small lake 0.5 mile southwest. To

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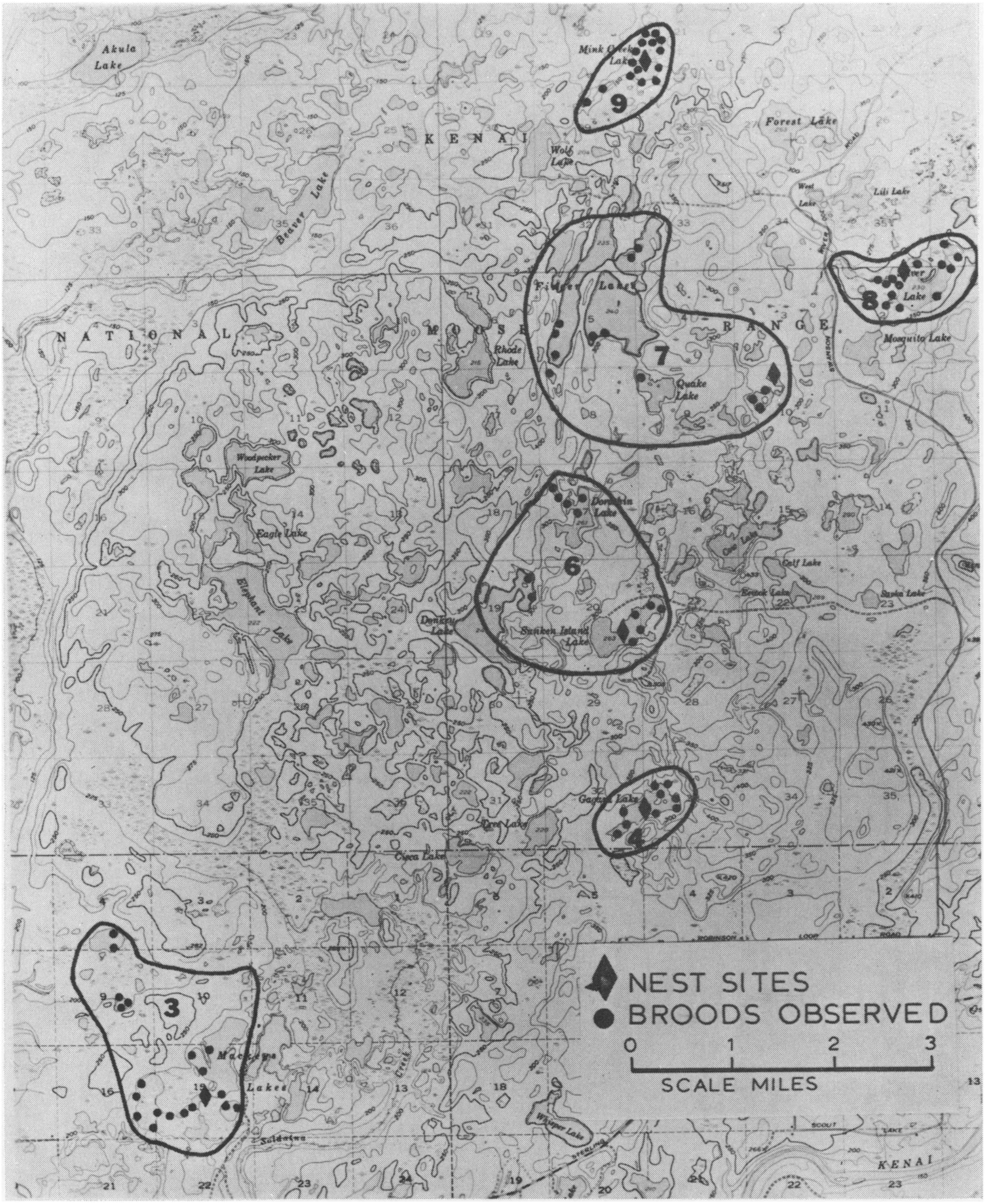

FIG. 33. Trumpeter swan brood movements in 1965 on the Kenai National Moose Range.

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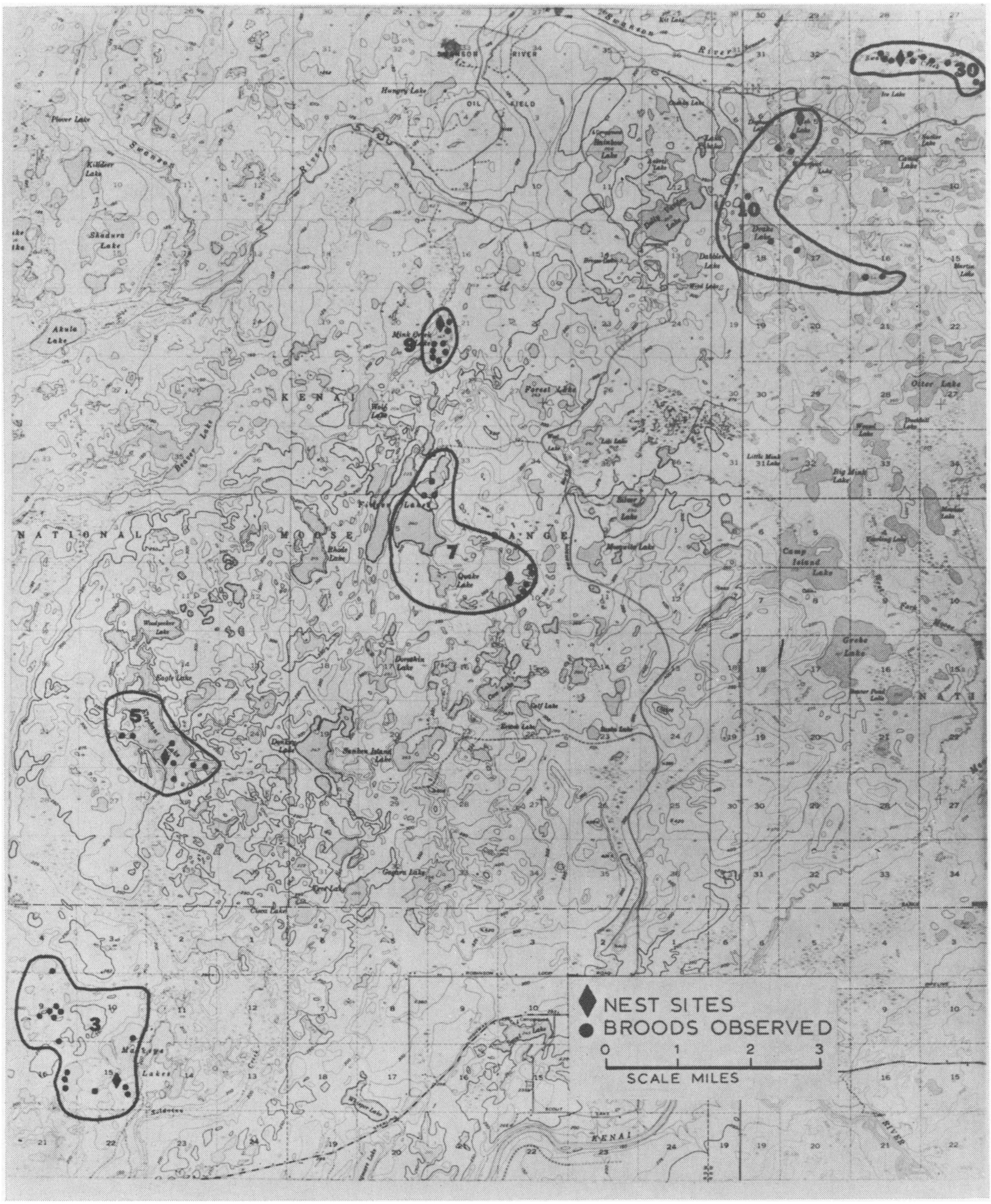

FIG. 34. Trumpeter swan brood movements in 1966 on the Kenai National Moose Range.

arrive at this location they had to cross a solid birch–spruce forest (Fig. 34).

In contrast, Pair No. 30, which nested on a stream, was never seen more than 2 miles from the nest site even though they could have traveled unrestricted up or down stream for several miles.

In 1965, 30 broods containing 151 cygnets

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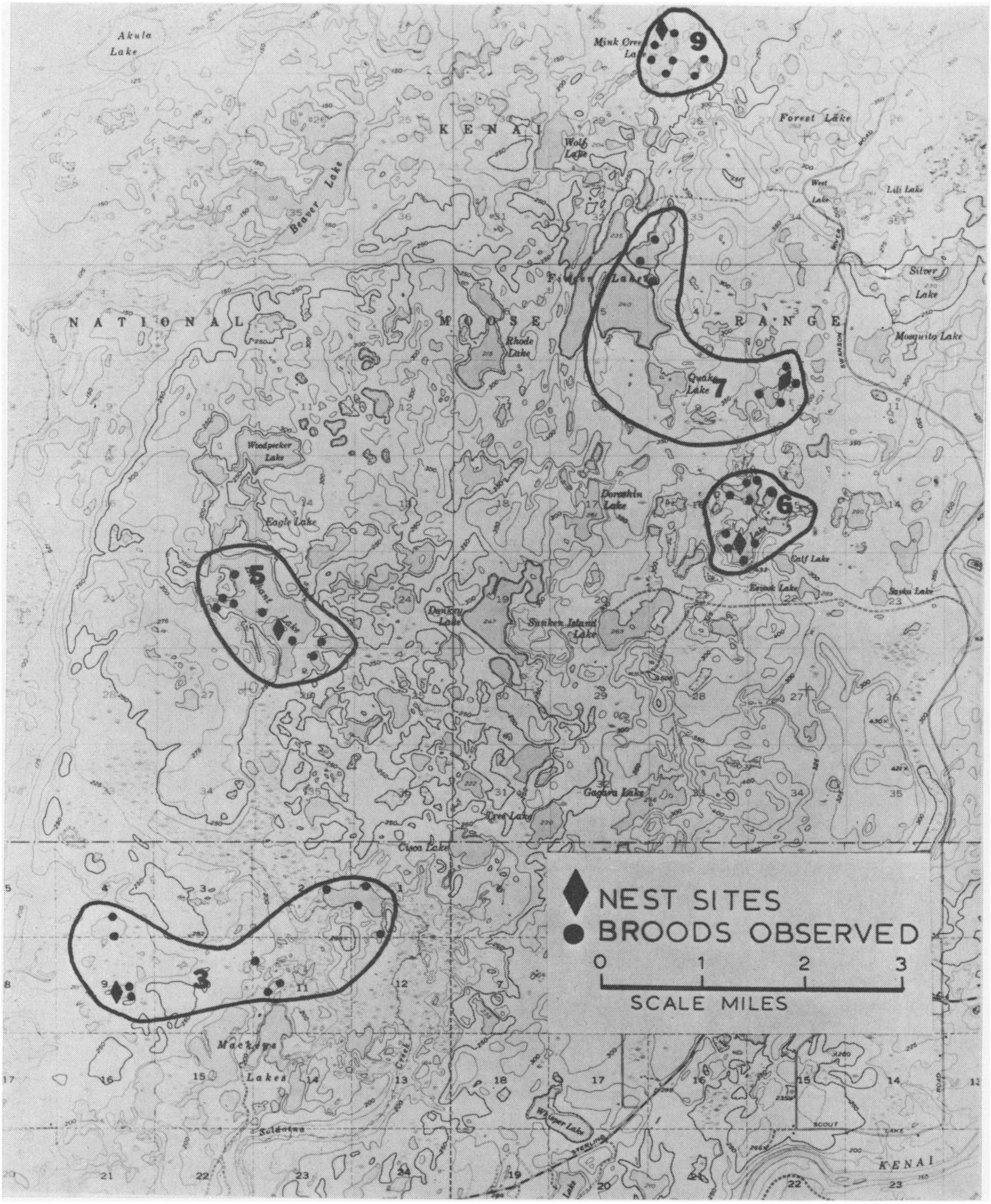

FIG. 35. Trumpeter swan brood movements in 1967 on the Kenai National Moose Range.

when hatched, still retained 121 cygnets by 9 September for an 80% survival rate. Nine broods incurred no mortality and none received total mortality. This exceedingly high survival rate occurred during the same year the greatest number of nests were recorded on the Kenai.

In 1966, out of 121 cygnets hatched in

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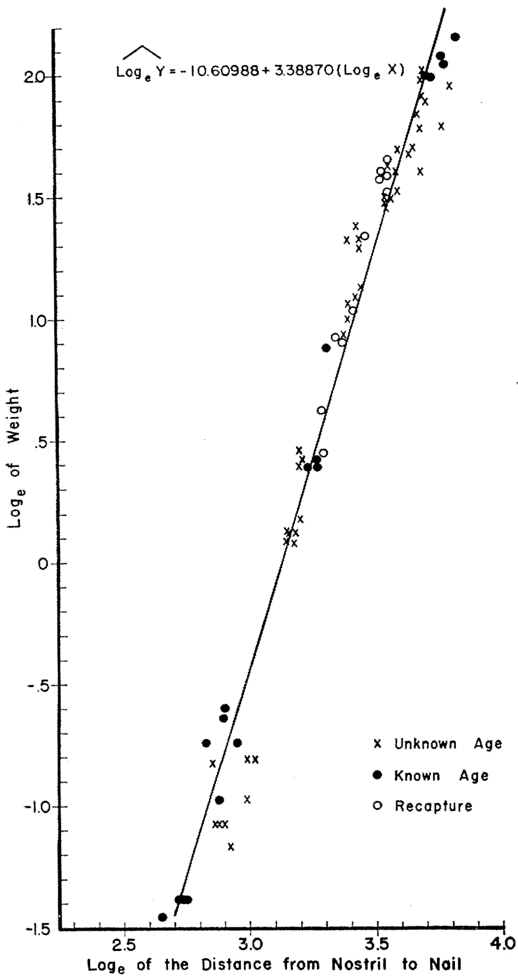

FIG. 36. Regression of cygnet weights in kilograms over distance from nostril-to-nail measurements in millimeters, connected to base logs.

28 broods on the Kenai, 86 survived to flight stage (71%). Two pair lost their entire broods but 9 pair did not lose any young. Three broods could not be located prior to flight stage. Eight of these broods, containing 35 cygnets at hatching, were counted repeatedly to determine the mortality in 10-day periods. One cygnet was lost in the first 10-day period, 3 in the second, none in the third, 4 in the fourth, and only one after the first 6 weeks.

In 1967, 18 broods containing 71 cygnets when hatched, had a survival of 55 cygnets

TABLE 16.—CYGNET AGE GROUPS BY FEATHER DEVELOPMENT AND BODY WEIGHT OF TRUMPETER SWANS IN ALASKA

Age Class by Feather Development[1]	Weight in Pounds	Age in Days	Midpoint Age in Days
Ia	0– 1	1–10	5
b	1– 2	11–17	14
c	3– 5	18–20	21
IIa	6– 9	29–38	35
—	10–12	39–45	42
b	12–14	46–52	49
c	15–19	53–59	56
III	——	60 or over	—

[1] Based on Gollop and Marshall (1954).

(77%). Of these 18 broods, 11 had no mortality and 2 had total mortality. As in 1966, 3 broods could not be located prior to flight, and they may have sustained some mortality also.

As on the Copper River areas, the cause of mortality was not determined. There seemed to be no definite pattern in the age at which most mortality occurred on the Kenai in contrast to the early loss incurred on the Lower Copper River. Observations on the Kenai indicated that cygnets often disappeared after they were at least one month old. Perhaps this could be attributed to more extensive brood movement progressing with age. It seemed likely that most of the mortality could have been credited to predators although some losses may also have been due to cygnets getting lost while families moved through forests. In 1966, a lone cygnet, which apparently had been permanently separated from the parents, was seen near Nest Lake for a period of several weeks. Another such observation was made at Finger Lake. Both cygnets were about 6 weeks old when first seen alone, and appeared to be surviving.

Feeding

Banko (1960) reported that feeding is confined largely to insects and aquatic invertebrates the first few weeks of the swan's life. Collections on the Bremner River revealed that invertebrates were abundant

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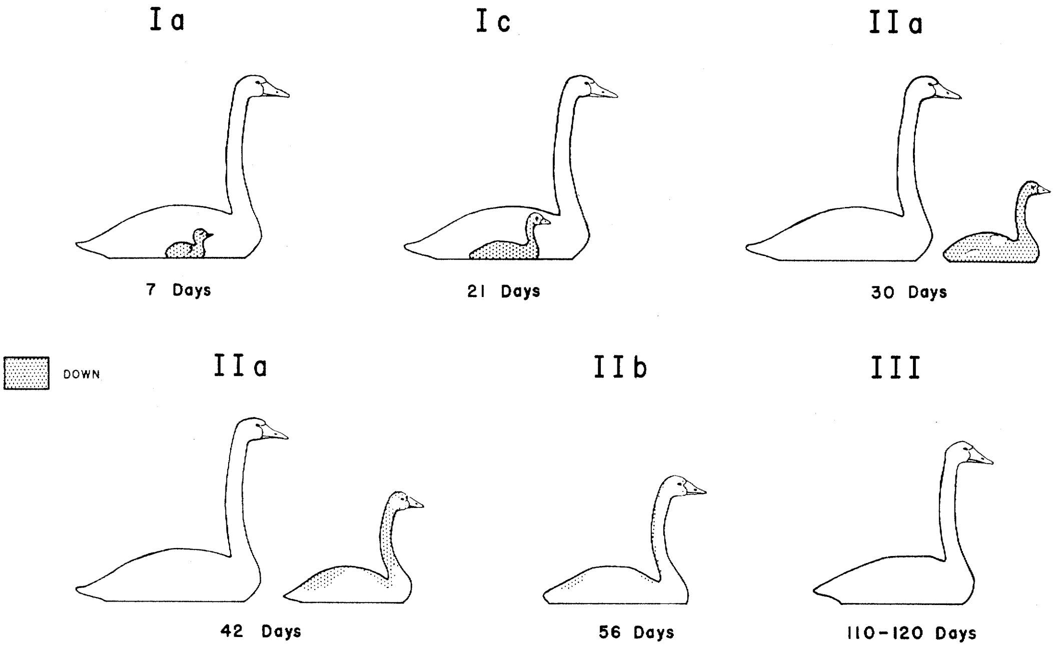

FIG. 37. Feather development and growth of the trumpeter swan cygnet in Alaska.

during the early brood period. Furthermore, cursory examination of cygnet feces in abandoned nests indicated a heavy use of insects and crustaceans.

Periodic visits to one nest site revealed that cygnets were feeding on vegetation before they were 2 weeks old. These young swans were seen feeding on *Equisetum fluviatile*. The cygnets fed on this coarse emergent by grasping the distal end of the stem about 6 to 10 inches from the tip and breaking it off with a twisting motion of the head. A drink of water was taken after every mouthful of food. This was accomplished by dipping the bill into the water and then raising the head and neck, chicken like, in a perpendicular position. These cygnets were noted to mimic every move the adults made in feeding and/or drinking.

Feather Development and Growth

Growth of trumpeter swan cygnets was amazingly rapid. Cygnets weighing less than 8 oz at hatching reached 19 lb in 8 to 10 weeks. The correlation of body weight to age was good up to 8 weeks of age. After 8 weeks, cygnets of the same age varied markedly in weight.

Certain skeletal measurements, especially bill measurements, were less variable. The relationship of cygnet weight in kilograms to the nostril-to-nail measurement in millimeters is illustrated in Fig. 36. The correlation coefficient of this regression was +.987, indicating a near perfect relationship between these measurements. An estimate of the age of all cygnets caught during the study was calculated by plotting known age broods against this regression. The resulting age groups were useful in establishing feather development classes (Table 16). A more realistic regression would involve the use of all 3 parameters: (1) weight, (2) bill measurement, and (3) age.

The Alaska trumpeter swan is fully feathered at 9 to 10 weeks, but cygnets are unable to fly before 13 weeks of age and some individuals not until 15 weeks, or between 90 and 105 days after hatching. Feather

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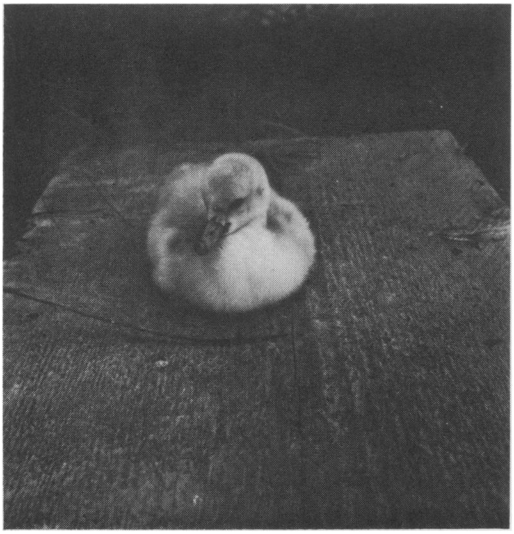

FIG. 38. One-day-old cygnet, Site 3, Peninsula Lake. Note egg tooth and down covered lores. (Photo by Shepherd)

FIG. 40. Partially feathered 42-day-old cygnet. Lores nearly bare at this age and typical trumpeter swan profile already well developed. Note stainless steel, lock-on band. (Photo by Shepherd)

development and growth is illustrated in Fig. 37. Photographs of 1-day, 21-day, 42-day, and 70-day cygnets are presented in Figs. 38 to 41, respectively.

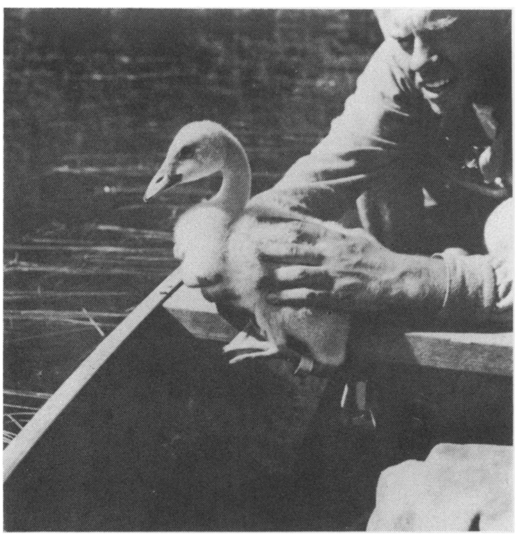

FIG. 39. Cygnet twenty-one days old. Leg has already developed sufficently to hold standard Size 9 band. First banded in 1957, this swan was recaptured in 1958 and again in 1959. (Photo by Shepherd)

Feathers begin to appear on the scapulars, flanks, and tail of the cygnet at the age of 4 weeks. This early plumage is followed at 5 weeks by feathering of the sides and belly, and partial feathering of

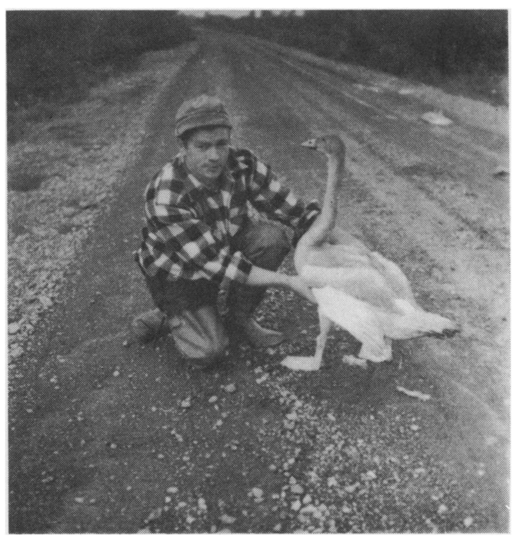

FIG. 41. Well feathered 70-day-old cygnet. Down still persists on nape and rump. (Photo by Shepherd)

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FIG. 42. Family of trumpeter swans on the Copper River Delta, 14 April 1969. The 10-month-old cygnet still retains its dark plumage, contrasting markedly with the adults. (Photo by Loyal Johnson, Alaska Department of Fish and Game)

the cheeks and neck. As the cygnet nears 6 weeks, the tail feathers erupt from the sheaths, the tail coverts become visible, and the lore becomes bare.

At 6 weeks of age the belly, breast, and cheeks are fully feathered. The neck and crown are partially feathered. The secondaries erupt from the feather sheaths, the tail and tail coverts are fully developed, and the sheaths of the primaries and primary coverts are visible.

The 7-week-old cygnet has added feathers to the upper back, most of the neck, and crown. There is still down on the nape, crown, rump, and under the wings. Secondary coverts have grown to 105 mm and the primaries to 100 mm. The greater and middle upper wing coverts are visible. By 8 weeks there is little down left on the body, except on the nape and lesser upper wing coverts. The rump is covered with down to the middle of the back. The primaries are from 160 to 180 mm long, the alula feathers are visible, and the underwing coverts emerge from their sheaths. A 9- to 10-week-old cygnet is fully feathered, but may still have some visible down on the rump and underwing coverts. The wing feathers are not yet completely grown at this stage.

Adult Molt

Information in the literature on molt of trumpeter swans is limited. Therefore, detailed notes were kept on feather molt of this species during the Alaskan study. Immature and adult swans regularly undergo an annual molt during the summer which

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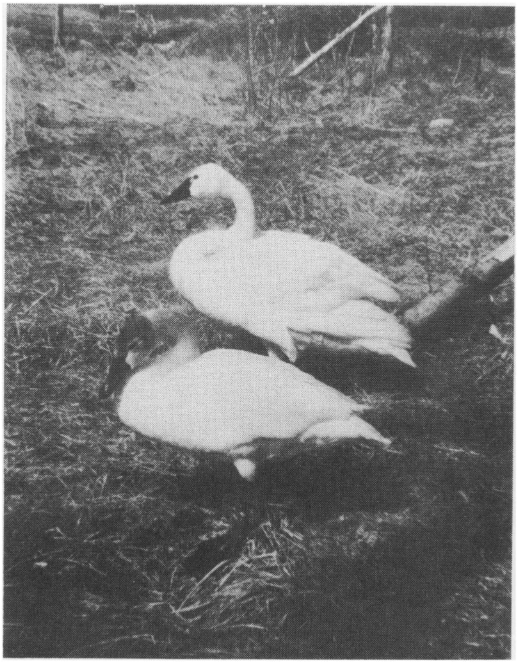

FIG. 43. Adult and cygnet whistling swans at Juneau, 24 April 1969. The 9½-month-old cygnet still retains dark feathers only on the head and upper neck in contrast to the trumpeter cygnet in Fig. 42. Note the yellow lore on the adult swan in the background. (Photo by King)

includes the loss and renewal of flight feathers (with the possible exception of the rectrices) and a partial contour feather molt.

Recovery of color-marked swans demonstrated that not all the tail feathers or body feathers were molted during the summer flightless period. Moreover, the greater secondary wing coverts appeared to be retained through this molt. Primary feathers, molted over a period of a few days, were preceded by the loss of the alula, and often many of the secondaries. Loss of flight followed the molt of a few secondaries and the alula.

A rusty coloration was common on the crown, cheeks, and nape of adult and immature trumpeter swans. These feather tracts were not pigmented, but stained from feeding in water rich in iron ions. The discoloration results from oxidation of these ions in the air, forming a ferrous stain (Höhn 1955). The breast, belly, and sides of the swan were also colored by this stain at times.

Plumages of trumpeter swans were generally pure white after they had completed their first molt at the age of 12 to 13 months. The few juvenile feathers some swans may have retained into their second year were on the lower back, rectrices, and secondary coverts. When young trumpeter swans retain enough of their gray yearling plumage that they are readily distinguishable from white adults without a particularly close scrutiny from the air (Fig. 42). In contrast, whistling swans at the age of 10 months are so nearly all-white as to be indistinguishable from adults (Fig. 43).

In late June or early July the nonbreeding adults gathered in flocks on large, open lakes and began the summer flightless period. This wing molt was more or less simultaneous among the nonbreeders, with all the swans starting and completing their primary molt within 7 to 10 days of each other (Fig. 44).

Nesting adult swans did not follow a regular molting sequence. There was a differential timing between males and females (Fig. 45). Rarely were both members of a breeding pair flightless at the same time (Table 17). The female began wing molt from 7 to 21 days after the eggs hatched. When nests were destroyed and the normal breeding cycle terminated prematurely, the female initiated molt soon thereafter, whether or not her mate was still flightless. This suggesed that the molt may be tied physiologically to the egg-laying and incubation cycle.

Males of successful nesting pairs appeared to molt either before or after the hatching period on the Copper River study areas (usually before). On the Kenai, all males under observation preceded their mates in the molt, usually starting early in the incubation period. The reason for a different molting pattern in male swans between the 2 areas was not determined, although the age of males may be a factor in regulating

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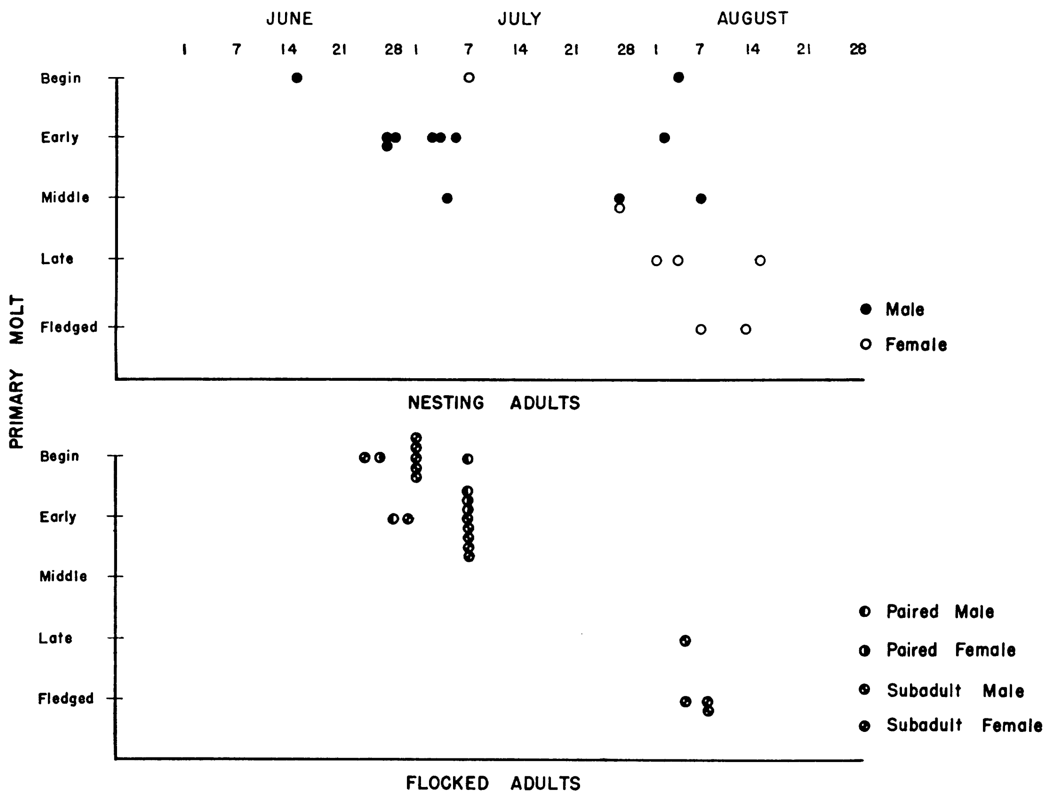

FIG. 44. Comparison of molt periods between nesting adults and nonbreeder flocks of trumpeter swans.

their molt, the older birds being earlier and more regular.

It is remarkable that the molt of successful breeders extended from mid-June to early September, over twice as long as the molt period of nonbreeders. A convenient feature of this extended molt period for the researcher was that a full range of swans by sex, age, and breeding condition could readily be captured when flightless for examination, banding, and color marking (Fig. 46). Both breeding swans and idle nonbreeders remained flightless for an average of 30 days after shedding their primaries.

Fall Departure

By mid-October, all the swans have departed from the Kenai Peninsula except for the occasional family group which may winter in the area. These could be late broods which did not attain flight age ahead of winter. Adults with broods probably remain later than nonbreeders in the normal course of events, because there are wide differences in flight attainment among cygnets of individual family groups.

An example of this was observed on the Kenai in 1959. A family was kept under

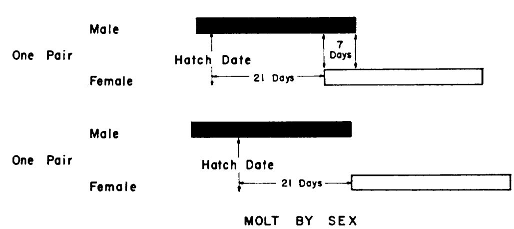

FIG. 45. Differential molt between breeding pairs.

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TABLE 17.—SEQUENCE OF WING MOLT, PAIRED AND NESTING ADULT TRUMPETER SWANS

Site[a]	Sex	Date Captured	Approximate Date of Hatch	Age of Young	No. of Days After Hatching	Primary Molt[b] Begin	Early	Middle	Late	Fledge	Mate Molting	Estimated Date of Fledging
4	M	6/15/59	7/9	9	-25[c]	X	—	—	—	—	No	7/14
UK	M	6/27/59	6/24	3	-4	—	X	—	—	—	No	7/19
28.5	M	6/27/59	Nest destroyed			—	X	—	—	—	No	7/19
SP	M	7/5/59	6/29	7	-7	—	—	X	—	—	No	7/21
UK	F	7/27/59	6/24	33	19	—	—	X	—	—	No	8/12
LK	M	7/27/59	6/18	39	23	—	—	X	—	—	Yes	8/12
SP	F	9/31/59	6/29	33	11	—	—	—	X	—	No	8/9
8	F	8/5/59	7/3	33	11	—	—	—	X	—	No	8/14
8	M	7/4/58	6/20	14	7	—	X	—	—	—	No	7/26
3a	F	7/7/58	6/17	20	20	X	—	—	—	—	No	8/5
3	M	7/7/58	—	—	—	—	X	—	—	—	No	7/28
SP	M	8/2/58	—	—	—	—	X	—	—	—	No	8/23
LK	M	8/4/58	6/9	56	55	X	—	—	—	—	No	9/4
UK	M	8/6/58	6/16	51	41	—	—	X	—	—	No	8/20
10	M	7/3/58	Nest destroyed			—	X	—	—	—	No	7/24
3	F	8/15/57	7/2	44	13	—	—	—	X	—	No	8/24
1	F	8/13/57	7/7	34	7	—	—	—	—	X	No	8/13

[a] Numbers 1, 3, 3a, 4, and 8 are all ponds or lakes on the Bremner River; 28.5 is the mile on the Copper Highway; abbreviations UK, SP, and LK stand for Upper King Salmon Slough, Storey Slough Pond, and Lower King Salmon, respectively.
[b] Based on length of primary feathers.
[c] Minus (–) refers to days before hatching when primary molt began.

close observation in early October. Some of the cygnets of this brood were still unable to fly when freeze-up eventually occurred on 13 October. During the crucial period prior to freeze-up, the actions of the birds indicated that the adults were trying to "teach" the young to fly. When all the young of this brood were able to fly, they departed the area together on or about 20 October.

Trumpeter swans, of necessity, must depart from all interior areas at least as early as they do from the Kenai and in most years by the first week in October to avoid total freeze-up. In some areas they may be able to linger where they have access to spring-fed streams or open rivers. On the Copper Delta, however, autumn remains longer and so do the swans. They are the latest of the migrant waterfowl to depart from the Copper Delta, many remaining there until mid-November, or a little later as a rule. It is possible that these are family groups which have moved somewhat leisurely, ahead of freeze-up, down the Copper River from the interior areas and across Prince William Sound from the Kenai–Susitna Basin to rest and feed on the Copper Delta as long as possible prior to migrating on down the coast. The longer that migration can be safely postponed, the better chance the cygnets have to survive the somewhat rigorous trip.

DISTRIBUTION AND POPULATION STATUS

The literature concerning the distribution and abundance of the trumpeter swan in Alaska is limited and brief, a fact that can be partially attributed to the inability of observers to distinguish the whistling swan from the trumpeter swan in the field. More likely is the possibility that trumpeter swans were few in number in the coastal areas traversed by the earlier naturalists and the species may have been largely depleted, due to hunting on much of its wintering grounds, by the time scientists extended their studies to the interior of Alaska. Another major reason for sparse records was the difficulty of summer travel prior to the advent of the small floatplane.

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Until shortly before World War II, vehicular travel in Alaska was restricted to a very scant road and railroad system. More extensive land travel was possible in the winter by dog team and snowshoes, but summer travel off the roads was restricted largely to riverboats. The aborigines and other early trappers and travelers ranged widely over the lowlands in winter, but as the snow and ice disappeared in the spring, human travel in areas of waterfowl habitat became greatly restricted. Muskrat hunters (the efficiency of shooting rats is preferred to trapping) in lightweight canoes frequented parts of what is now recognized as trumpeter swan habitat for a short period following spring breakup. By the time swans would have hatched, however, all human activity would have been concentrated along the rivers for salmon fishing and other summer endeavors. Thus, for most of the summer the vast majority of the trumpeter swan's nesting habitat remained completely undisturbed and unvisited by man.

An accurate record of trumpeter swan distribution and a reasonable estimate of its numerical status in Alaska could not be compiled until the airborne biologist became active. The first such waterfowl position was established with the arrival of the senior author in 1954. Trumpeter swan observations began to accumulate soon thereafter as interest was generated among the Fish and Wildlife Service field force.

Distribution

Early Knowledge

Banko (1960) cited all the available literature on trumpeter swan distribution. We have made no effort to duplicate his exhaustive review of those records pertaining to Alaska and Arctic Canada except to try and interpret some of the early information in light of knowledge derived from our recent studies.

It appears that the first published comment on the trumpeter swan in Alaska was that of Dr. Edward Adams (1878) an English ornithologist, who made the following observation during the period 1850–1851: "*Cygnus buccinator*. This was the only species I met with at Michalaski (St. Michael). The first appeared on the 30th of May; but they were at no time numerous, from two to eight or ten keeping together. A few of them are said to breed here; but most of them go further north."

FIG. 46. Group of 3 flightless yearling trumpeter swans from same brood, recaptured on natal marsh. Note the minimum restraint necessary to control these birds after having failed in their strenuous escape effort. (Photo by Shepherd)

Banko (1960) stated that, although later writers either overlooked this account or believed Adams had confused the whistling swan with the trumpeter swan, subsequent egg records of trumpeter swan in the Norton Sound area strengthened Dr. Adams' original statement. Trumpeter swan eggs belonging to the R. M. Barnes collection at the Chicago Natural History Museum were collected 28 June 1902, 38 miles northeast of Cape Nome by Walter E. Bryant. Another egg (one of 2) collected by J. B. Chappel in 1867, in Norton Sound near Cape Denbigh, is in the United States National Museum. A clutch of 5 eggs collected on 4 June 1915 at Bethel, Alaska, by A. H. Twitchell (originally identified as whis-

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tling swan eggs) were examined by Banko and found to be trumpeter swan eggs.

Dall and Bannister (1869) recorded that eggs of the trumpeter swan were obtained by a Mr. Lockhart at Fort Yukon, thus establishing the first definite breeding record for this species in Alaska. The United States National Museum has on deposit one of these eggs, received in April or May 1863 (Banko 1960).

Of significance in perusal of early records is the lack of any notes regarding breeding birds south of the Alaska Range. This is noteworthy since the present centers of high density are in the south-central area which, during the late nineteenth century and early twentieth century, was literally swarming with prospectors, trappers, and government survey personnel. In fact, no mention of swans is found in Abercrombie's (1899) bird lists of the Copper River Valley, nor in any subsequent geological investigations of the Hanagita–Bremner regions (Moffit 1914). That such an obvious bird as a swan could have been overlooked by anyone, let alone competent naturalists and ornithologists, seems unlikely and suggests that few if any swans were nesting in this area during the given period.

Current Knowledge

Verified Records.—Notes and published literature since 1920 provide a much richer source of information regarding distribution, abundance, and breeding than the earlier records. Banko (1960) quoted a report by E. L. Kepner which he found in the United States Fish and Wildlife Service files dated 8 March 1924, as follows:

"Camp Kora Kora; Lake Minchumina, Kantishna District. This low lying section of the interior is especially adapted to the waterfowl—the great white Trumpeter Swan is the least plentiful of all the species, but he is also in evidence in goodly numbers, and I have also noticed the hunters after it—I believe the Treaty regulations between the U. S. and the Dominion of Canada afford them all the protection required. Lake Minchumina appears to be a favored spot for them to stop over and feed and rest on their northern and southern migration."

Lake Minchumina is in the interior of Alaska approximately 75 miles northwest of Mt. McKinley (64° N). Kepner's report suggests that a breeding population was in existence at least 50 years ago in this geographic area.

Otto Koppen, a long-time Fish and Wildlife Service employee and permanent resident of Cordova and south-central Alaska, revealed that as early as 1924, adult and young swans were wintering with green-winged teal (*Anas carolinensis*), American widgeon (*Mareca americana*), and pintail (*Anas acuta*) in open "grassy" springs near the Tisu and Kalikh rivers. Mr. Koppen also saw swans during the winter on Bering River and Sand River. These locations are approximately 50 to 100 miles east of Cordova, Alaska.

No further observations or published material are available for the next 10 years. In about 1934 or 1935, George Nygengast of Chitna, Alaska, while trapping muskrats near the mouth of the Bremner River (Fig. 2), witnessed the courtship and copulation of a pair of swans in early May. He said that he was able to recognize these birds as trumpeter swans by their resonant trumpeting. From his observation and detailed description, copulation would appear to be carried out in the same manner as with geese. These birds were frequenting one of the few open water areas to be found at that time of year (pers. comm. 12 June 1958).

Monson (1956) stated that 2 swans, positively identified as trumpeters, were killed in 1949 on the Chickaloon Flats of the Kenai Peninsula. Frank Glaser, former employee of the United States Fish and Wildlife Service, reported seeing a pair of trumpeter swans with cygnets on the Gulkana River, 15 September 1952. He identified these as trumpeters by their call.

Mrs. Alda Orton (1951) reported a small number of breeding trumpeter swans on

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the lakes of the Naha River Valley near Ketchikan in southeastern Alaska. This published account has been cited as representing the first breeding record for southeastern Alaska. A recent investigation of this account discredits the original version, however. The swan families about which Mrs. Orton wrote were winter visitors on the lower Naha River. She assumed that they had been raised on the headwater lake of the Naha without having seen them as flightless cygnets.

During June and July 1952, Charles Trainer, U. S. Fish and Wildlife Service biologist, saw immature swans on Martin River Slough and 6 additional adults near Cottonwood Point. Both locations are on the east bank of the Copper River near its mouth.

Wildlife authorities did not become fully aware of the presence of a substantial breeding population of trumpeter swans in south-central Alaska until a broad program of field work in the lower Copper River Basin was initiated during the summer of 1954. A complete aerial census of the Tasnuna and Bremner river valleys, made in conjunction with salmon surveys during mid-August of 1955, revealed 69 adult swans and 5 broods totaling 15 cygnets. Identification of this population as trumpeter swans was verified on the ground through measurements of eggs (Monson 1956). This discovery was the impetus needed to initiate trumpeter swan investigations on the Bremner River and the Kenai National Moose Range. Data from the first Kenai survey in 1957 revealed that 20 pairs of swans nested on the Kenai National Moose Range, and 10 nonbreeders resided in the area. Measurements of 3 clutches of eggs fell well within the trumpeter swan size range and an adult male swan was collected and identified by autopsy as a trumpeter swan, thereby verifying the addition of another breeding population of trumpeter swans.

Ground observations of swans on the Bremner River and the Copper Delta during the summer of 1957 further substantiated Monson's findings. It was assumed at the time that most or nearly all of the nesting swans in these areas were trumpeters. The criteria upon which this assumption was based included one or more of the following: (1) measurements and weights of adult birds; (2) voice characteristics; and (3) a limited egg collection (7 eggs).

On 12 April and again on 26 April 1957, Bob L. Burkholder, Fish and Wildlife Service biologist, counted 54 swans on Old Man Lake near Glennallen. Burkholder tentatively identified 44 of these as trumpeter swans, based on "size, wing beat, and voice." Spurred by the possibility of nesting trumpeter swans in a new location, Hansen found 6 nest sites, 5 single swans, and 8 swans in a flock in this general area on 12 June 1958. He was able to confirm the identity of 2 nesting pair as trumpeters by egg measurements (Fig. 10).

On 10 May 1958, U. S. Game Management Agent Jim H. Branson censused the swan population along the Kustatan and Drift rivers on the west side of Cook Inlet. He counted 112 swans, including 34 adult pairs of which 15 pairs were definitely nesting. A flock of 43 yearlings was also counted and egg counts made on 6 nests. Branson stated that the type of nest site and nest construction led him to assume the birds were trumpeter swans. Later the same summer (19 August), Hansen counted 9 broods totaling 43 cygnets in the Kustatan–Drift River area. These observations added another probable breeding population, thus extending the trumpeter swan's known breeding area over nearly the entire south-central geographic region.

Unverified but probable breeding records of trumpeter swans were made by Hansen and King during the summer of 1959 in the Tanana Valley near Minto, about 50 air miles west of Fairbanks. Identification was tentatively based on nest site and construction characteristic of trumpeter swan nests on the Lower Copper River. Positive

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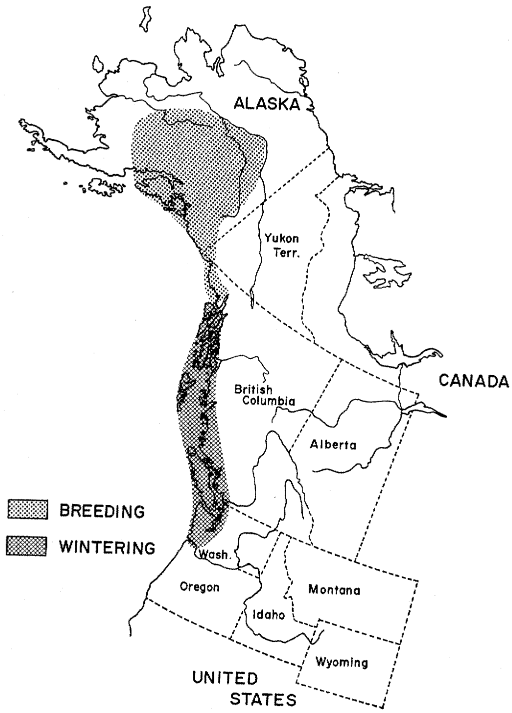

FIG. 47. The known major breeding and wintering distribution of Alaska's trumpeter swans.

identification was made in the summer of 1960 when 9 swans, both adults and cygnets, were captured and banded in this area by King and Shepherd. This population extended all the way up the Kantishna River valley to Lake Minchumina, the area of Kepner's 1924 citation.

With the newly acquired ability to identify trumpeter swan nests from the air, we were encouraged to scan all swan populations more carefully during the routine aerial waterfowl census each spring. In this manner, as well as further ground reconnaissance and special aerial surveys, trumpeter swans have been identified over a wide area including occasional nest sites near the early historical Bering Sea coast records.

On 30 May and 2 June 1958, swans were observed sitting on or near typical "donut"-shaped trumpeter nests near Bethel on the Yukon–Kuskokwim Delta and in the Noatak Valley about 40 miles north of Kotzebue. On 31 May 1962, a typical trumpeter nest with a swan sitting on it was observed near the head of Igiak Bay approximately halfway between Bethel and St. Michael on the Yukon Delta. During a routine banding operation on the Dall River near Stevens Village in August 1960, King observed a pair of swans at close range on the ground and identified them as trumpeters by their call. They had one cygnet with them and a nest was located in a marsh about one-half mile distant. In 1969, Dr. James Bartonek saw a pair of swans with a brood of 4 in this area and in 1970 Bartonek and King observed a pair with 4 young on the same lake. In addition to the family of swans there were 2 groups of 3 adults each on a nearby lake. A thorough search of this general area produced no other swans. Stevens Village lies approximately 100 miles downstream from Ft. Yukon where the first definite breeding record for trumpeter swan in Alaska was established in 1863.

On 19 May 1965, King observed a swan on a nest at Sand Lake on the upper Tanana River with its mate nearby. Sand Lake is 50 miles east of Big Delta and approximately 100 miles west of the Canadian border. This is the farthest east nest record in central Alaska and the only record in the Tanana Valley east of Blair Lake which lies 35 miles southeast of Fairbanks. There have been no swans observed in this vicinity since 1965.

Discounting the dubious Naha Lakes record (Orton 1951), there have since been 2 authenticated trumpeter swan breeding records for southeastern Alaska. On 11 September 1967, King and Game Management Agent Fred C. Robards saw a pair of swans with cygnets in the Chilkat Valley 15 miles northwest of Haines. On 8 June 1969 on the same lake, King observed an incubating swan on a typical trumpeter nest. There is the possibility of more extensive nesting in southeastern Alaska inasmuch as there is a considerable amount of habitat which has not yet been searched.

The distribution of the Alaska trumpeter swan is shown in Fig. 47.

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Theoretical Limit of Breeding Range.—From many years of field study, numerous observers assumed, and accepted as fact, that waterfowl develop at an accelerated rate under the long hours of daylight in the arctic and subarctic summer. To test this theory, Karl Schneider (1965, unpublished master's thesis, University of Alaska, College, Alaska) studied the growth and plumage development of 4 species of ducks under natural field conditions near Tetlin, Alaska, (61°N; 142°30′W). The growth rates of mallard, canvasback, scaup, and bufflehead was compared with the same species in comparable studies conducted on the southern prairies (Gollop and Marshall 1954).

Based on Schneider's work it appears that accelerated development leading to early attainment of flight in a northern environment, in the 4 species studied at least, may be little more than an optical illusion. Schneider (unpublished master's thesis) concluded that: "A comparison of the average rates of plumage development of ducklings observed at Tetlin in the present study with the average rates observed in southern Canada and the northern United States by other investigators . . . does not substantiate the idea that northern ducklings have faster rates of plumage development than southern ducklings of the same species. The rate of feathering of northern birds, apparently, can be faster, slower, or the same as southern birds. For the purpose of this discussion, the rate of plumage development is considered to be the time between hatching and the attainment of flight. The rate of body feathering is considered to be the time from the first appearance of juvenile feathers on the side of the body to the time when no down is visible under field conditions. In other words, the rate of plumage development involves Classes I, II, and III, whereas the rate of feathering involves only Class II."

These conclusions are somewhat at odds with the differential rate of trumpeter swan development between Red Rock Lakes and Alaska populations. From the date of hatching, trumpeter cygnets in Alaska require from 90 to 105 days to become fully fledged and on the wing. This compares with a developmental period of from 100 to 120 days for Red Rock Lakes cygnets (Banko 1960). It would be desirable to explore this growth rate problem in greater depth with a wider array of species to clarify these divergent findings. It is of particular significance with respect to the northward extension of range of a species requiring a long period for growth such as the trumpeter swan.

In addition to the 90 to 105 days required for Alaska cygnets to become fledged, an average of 49 days is used for nest building, egg laying, and incubation. Thus, a minimum of 140, and up to 154, ice-free days are necessary for trumpeter swans to complete a reproductive cycle successfully under northern conditions. Using a 145- to 150-day span between breakup and freeze-up, we have reconstructed the theoretical northern limits of the trumpeter swan's breeding range across North America.

Standard, universal definitions of the terms "breakup" and "freeze-up" are not available in the literature. We were interested in the period of ice-free time a shallow body of water would be available for the nesting and rearing of trumpeter swans (150 days), as opposed to ice conditions suitable for foot travel or open water for commercial use, the usual basis for defining breakup and freeze-up. For purposes of this study, then, breakup is the date when ice moves in a river or clears from the shore of shallow brood lakes, and freeze-up is the date when ice forms and begins to grow in shallow lakes.

Burbidge and Lauder (1957), Thompson (1963), Allen (1964), and other research meteorologists have developed criteria to show a correlation between mean air temperatures and the breakup and freeze-up phenomena. The breakup of ice in rivers is much earlier than the clearing of ice from large lakes because mechanical or

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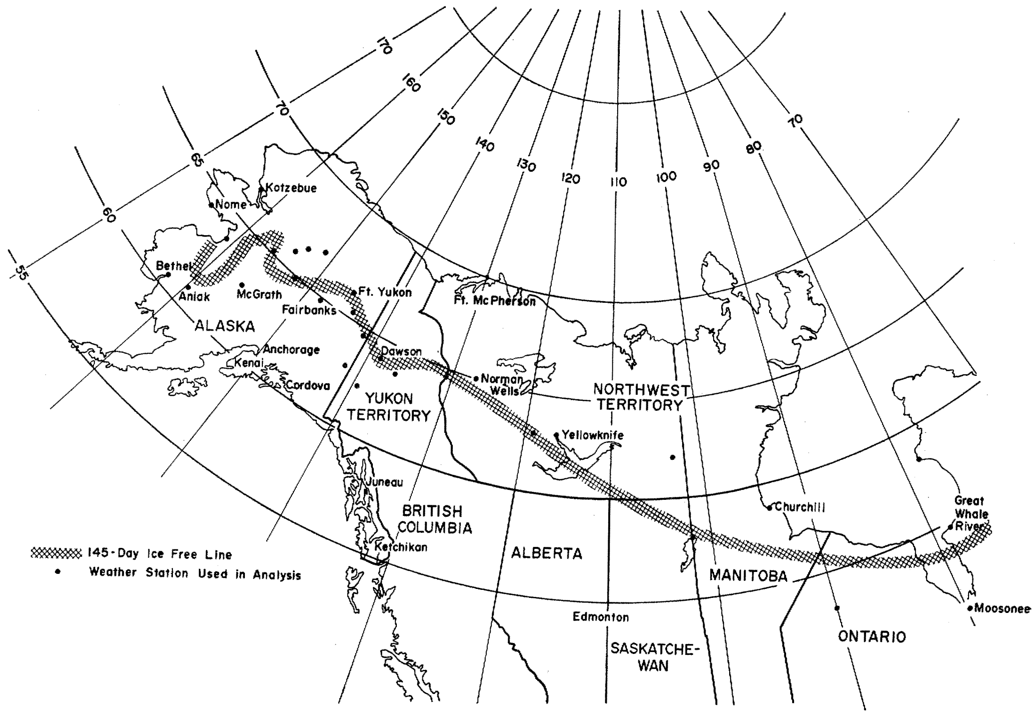

FIG. 48. The theoretical northern limit of the breeding range of trumpeter swans based on a 145- to 150-day ice-free period.

hydraulic forces start to work on river ice almost as soon as melt water appears from the surrounding land. Lakes are very slow to clear of ice in comparison with rivers since most of the lake ice must be cleared by the gradual process of melting. However, the melting of snow on the shores and runoff from surrounding land creates a narrow shore break well ahead of the final clearing. This shore break usually coincides with the breakup of rivers in the same area. Burbidge and Lauder (1957) determined that it requires 12 to 18 days (15-day average) with a mean daily temperature above 32 F. before ice moved out of 5 different rivers at widely distributed locations throughout northern Alberta, Yukon, and the Northwest Territories of Canada.

During the process of freeze-up there is a gradual loss of the residual summer heat so that by the time the mean daily temperature falls below 32 F skim ice forms and starts to grow on shallow lakes and sloughs within a day or two. The length of time for ice formation on rivers and large, deep lakes is considerably longer but varies from only a few days to several weeks depending upon current, volume of water, and degree of wind action.

The northern limit of a 145- to 150-day ice-free period is illustrated in Fig. 48. The isopleths across Canada west of Hudson's Bay were adapted from Allen (1964). Allen's method of calculation was used to determine the location of the isopleths on across Alaska based on mean temperatures compiled from U. S. Weather Bureau records from 16 Alaska stations. Where available, a period of 10 years for each station was used to compute mean temperatures from which breakup and freeze-up dates were calculated.

The shaded zone in Fig. 48, varying in width from 50 to 100 miles, indicates the limit of the breeding range wherein trumpeter swan cygnets can reach flight stage

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in favorable years; that is, a minimum ice-free period of 145 days. Successful production would not be possible in those unfavorable years which contribute equally with the good years to comprise the "mean." It is in this marginal area that a relatively few trumpeter swan nests have been identified from the air, but a stable breeding population apparently cannot sustain itself despite these pioneering efforts. The northern edge of this zone follows the Yukon River quite closely eastward from the Bering Sea all the way to Dawson, Yukon Territory, before veering off toward Great Bear Lake. The area north of the shaded zone is theoretically beyond the breeding range of the trumpeter swan. Although nesting records have been verified from this area we have no knowledge that cygnets from these nesting attempts became fledged and migrated successfully. The region south of the shaded zone should be environmentally suitable to sustain breeding populations wherever acceptable nesting habitat is available and adverse microclimates do not preclude nesting.

Known Wintering Range.—Gabrielson (1946) was told of swans wintering in southeastern Alaska in 1940 but had no opportunity to check the situation until March 1944 when he counted 300 swans from the air. He remarked that they "looked big," but was not able to make a positive identification at that time. In the same general area in January–February 1945, Dan H. Ralston, Fish and Wildlife Service Game Management Agent, counted 324 swans. Most of these were in the bays and freshwater lakes of the numerous islands between Petersburg and Ketchikan. Later that winter a dead swan found at Ward Lake, near Ketchikan, was identified by autopsy as a trumpeter. Subsequently, other trumpeter swans have been identified as far south as the mouth of the Columbia River.

Eklund (1946) added significantly to the record as follows: "On March 16, 1945, while on an Army maneuver in British Columbia, Canada, I found remains of a Trumpeter Swan (*Cygnus buccinator*), on the Bella Coola River, one-half mile west of Stuie . . . Positive identification was made by the presence of the trachea and the enlarged tracheal bulla in the skeletal remains . . . Exact date of the killing is unknown, but it is assumed to have occurred in midwinter. A census of Trumpeter Swans in February, 1945, at Tweedsmuir Park, adjacent to Stuie, showed 134 birds wintering in that area. The birds are in this country from November to March or April, and many are concentrated on Lonesome Lake near the southern tip of the park."

Tweedsmuir Park is located toward the interior of British Columbia from the coast and, thus these swans may well have been a wintering concentration of the trumpeters which breed in northern British Columbia rather than the Alaskan swan (Mackay 1954).

On 15 December 1959, a hunter found a dead banded bird on the delta of the Nanaimo River on the southeastern coast of Vancouver Island, British Columbia. When the hunter submitted the band to a game official, he identified the bird, which appeared to have been dead for several weeks, as a "Canada goose." The number reported (509–25012) was a band placed on a female trumpeter swan cygnet which had been colormarked with purple dye when banded on the Copper River Delta on 6 August 1958. On 26 November 1967, a hunter shot a swan (Band No. 509–63091) on the Ucona River on Vancouver Island. This bird had been banded as an adult female trumpeter swan 20 July 1960, on Martin Lake near the Copper River Delta.

During the winter months of 1969–1970 personnel of the British Columbia Fish and Wildlife Branch in cooperation with the Canadian Wildlife Service surveyed the swans wintering on Vancouver Island and part of the adjacent mainland. A total of 402 swans were counted on Vancouver Island and an additional 129 on the mainland.

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A comparison with earlier but less complete surveys indicated that the wintering population of trumpeter swans on Vancouver Island may be as many as 600 (Trumpeter Swan Society 1970).

Game Management Agent Lawrence C. Wills (pers. comm.) reported numerous flocks of swans, identified as trumpeters by their voice and size, wintering as far south as Grays Harbor in western Washington since 1966. Several of these birds have been shot (ostensibly as snow geese, during the open waterfowl seasons) 9 of which have been retrieved and identified as trumpeter swans. Most of the recovered specimens are currently in college and university collections.

Winter inventory counts have been only intermittent and cursory. Thus, they do not show population growth or give an accurate picture of relative abundance on the winter range. The variability in this coverage is due to many factors, the most important of which are size and physiography of the area, extreme high and low tides, and the generally inclement winter weather along the north Pacific Coast which greatly restricts both an extensive flight operation and survey by small vessel.

There is approximately 20,000 miles of rugged coastline in southeastern Alaska and British Columbia laced with innumerable fiords, tidal bays, and freshwater lakes. The swans are distributed over much of this vast area in family groups and small flocks. They move back and forth between the freshwater lakes and the saltchuck meadows at high tide as freezing conditions dictate. Much of their habitat is relatively inaccessible from the surface and even less so from the air because of swirling fog, rain, low clouds, and buffeting winds at the head of steep-canyoned, narrow bays.

Near the southern end of the wintering range, trumpeter and whistling swans undoubtedly commingle to an unknown degree, particularly along the lower Columbia River and possibly as far south as the Sacramento Valley of California. This would conform to their ancestral range as first identified by Lewis and Clark in the winter of 1805–1806 (Coues 1893), and by other observers half a century later (Suckley 1859, Newberry 1857, Heerman 1859).

Population Status

Current Numbers

In order to determine the approximate number of trumpeter swans in the vastness of Alaska and to document the growth of the population, extensive aerial surveys were necessary. The basic technique for conducting a total "head count" was worked out in August of 1958 on the intensive study area of the lower Copper River and in the Cook Inlet area near Anchorage. Although a total count was not achieved in this initial survey, 674 swans were found. A more intensive effort in 1959 produced 1,041 swans in the same areas surveyed the previous year, plus 83 more along the coast between the Bering River and Yakutat, for a total of 1,124 in south-central Alaska (Table 18).

In retrospect, we realized that some swans were missed and that an even more intensified effort would be needed to document accurately the distribution, abundance, and population growth of the trumpeter swan in Alaska. Unfortunately, 9 years elapsed before an adequate survey could be scheduled and conducted in August and September of 1968. The survey was standardized and recorded in such a manner that it can be duplicated by competent observers at any time in the future to collect comparative data. The basic survey maps and detailed tabulation of field data have been deposited in the Bureau of Sport Fisheries and Wildlife working file in Juneau, Alaska.

Four pilot–observer teams flew a total of 123.7 hr between 13 August and 13 September 1968, to complete the survey in the major geographic areas where nesting trumpeter swans have been identified exclusive of nesting whistling swans. This included a total area of 22,210 square miles of aquatic habitat. No attempt was made to

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TABLE 18.—ALASKA TRUMPETER SWAN AERIAL CENSUS COUNTS, AUGUST–SEPTEMBER 1959 AND 1968

Geographic Area	Size of Area (miles²)	Adult		Cygnet		Total	
		1959	1968	1959	1968	1959	1968
Kenai Peninsula	2,375	120	116	58	65	178	181
Cook Inlet–Susitna Basin	5,625	169	295	37	124	206	419
Gulkana Basin	5,500	50	400	19	190	69	590
Copper Canyon	190	119	114	28	44	147	158
Copper Delta–Gulf Coast	2,080	371	660	153	362	524	1,022
Tanana–Kantishna Valley	6,440		340		138		478
Total[1]	22,210	829	1,925	295	923	1,124	2,848

[1] Totals not directly comparable because of unequal coverage in some areas.

count trumpeter swans where the range of the 2 species overlaps because no reliable means of distinguishing between them from the air has been developed, except at a nest site as described earlier.

From the evidence at hand, we think that relatively few trumpeter swans invade the tundra environment of whistling swans even though a trumpeter nest has occasionally been identified from the air in that area. Extensive banding of many waterfowl species, including swans, on the Yukon–Kuskokwim Delta since 1949, and intensive waterfowl production studies each year in that area since 1962 have produced only one positive trumpeter swan brood identification among the many whistling swan broods observed from the ground. This was in 1968 during a routine banding operation not far from Igiak Bay where a trumpeter swan nest was identified from the air in 1962.

Swans are observed as pairs and in small flocks each spring during the routine waterfowl breeding population survey on the upper Kuskokwim River and some of its tributaries south and west of Lake Minchumina. We suspect that these may be a southward extension of the trumpeter population from the Kantishna River, which drains north into the Tanana, or they could be an inland intrusion of the Cook Inlet trumpeter swans seeking relief from the population pressures that have built in that area rather than an inland expansion of whistling swan from the Bering Sea coast.

In the Koyukuk Valley there is also a small resident population of swans. Over a 13-year period, while conducting waterfowl breeding population surveys in late May and early June, we have counted an average of 3.5 adult swans per year along 160 miles of standard transect line (one-eighth mile of habitat on each side of the airplane). During that span of time 3 trumpeter-like nests were observed. On that basis we have identified the Koyukuk Valley population as trumpeter swans. Because of the sparse numbers of birds and long distances involving these latter 2 populations, the areas were not included in the 1968 trumpeter swan survey. The extensive Yukon Flats was excluded from the survey as well because it had been surveyed earlier in the summer and no swans were found to justify a later search during the extensive integrated aerial survey.

As summarized in Table 18, 2,848 swans were tallied. From past ground studies in these areas and the general fund of knowledge accumulated about swans in Alaska, we have no hesitation in classifying virtually all swans as trumpeters. Even though the 1968 survey was more carefully planned and more thoroughly conducted than the 1959 survey, there is no question but that some swans were overlooked in both. An attempt was made to thoroughly search every suitable unit of swan habitat within the 22,210 square miles of the major areas. By late summer the cover was rank enough in places that some swans, particularly cygnets, could have hidden easily before the airplane was overhead.

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Visibility of waterfowl from the air varies markedly among species with visibility rates of up to 80% among the more conspicuous species of ducks (Martinson and Kaczynski 1967). If swans were accorded an extremely high visibility rate of 90%, there would have been 285 in addition to the 2,848 counted, for a total of 3,133. If, on the other hand, a more realistic visibility rate of 80% were used, there would have been a minimum of 3,400 trumpeter swans in Alaska in 1968.

Better coverage and more efficient techniques in 1968 undoubtedly located some birds in marshes where they were present in 1959 but not discovered at that time. How much of the increased count was due to an expanded population since 1959 and how much was the product of the more extensive and better survey in 1968 is speculative at this time. Both factors are involved, but unfortunately, a lack of comparability overall in the 2 surveys does not allow for a proper evaluation. For instance, the population on the Kenai and in the Copper River Canyon, 2 areas with comparable coverage during both surveys, was essentially the same in 1968 as it had been in 1959. By way of comparison, about 90% more swans were counted in 1968 along the Gulf Coast, 100% more in the Cook Inlet–Susitna Basin area, and 750% more in the Gulkana Basin.

The most important aspect of the 1968 survey is that it provided a solid baseline from which to measure extension of range, population growth, and population dynamics in future studies.

Growth Potential

The structure, or profile, of a swan population is one method of measuring its senescence or its potential for continued growth. Banko (1960) demonstrated that the population on the Red Rock Lakes Refuge had a high ratio of productive to idle adult pairs in its early stages of growth in an uncrowded environment. When the breeding habitat attained a saturation level, the total number of paired swans remained high but the ratio tipped in favor of idle pairs and average brood size declined 24%. During the period with a comparatively low breeding population (1936 to 1942), 74% of the paired swans observed had young with an average brood size of 3.7 cygnets. During the period with a high breeding population (1951 to 1957), only 39% of the paired swans observed had young with an average brood size of 2.8 cygnets.

The Red Rock Lakes population increased at a constant rate of about 10% annually from 1935 until 1954 at which time a definite leveling out became evident.

Judged against this background one might infer that trumpeter swan populations in Alaska have already achieved their growth potential, the vast area and countless unoccupied marshes notwithstanding. In 1968, the ratio overall of productive to idle pairs was 37.6% productive, ranging from a low of 29.6% in the Cook Inlet–Susitna Basin area to a high of only 48.8% on the Kenai Peninsula. On the other hand, the average brood size of 3.69 in Alaska in 1968 was as large as the average brood in the Red Rock Lakes area during the early growth years of that population (Table 19).

Upon termination of the survey in 1968, most of the participants were of the opinion that, even though the swans were widely scattered and many water areas were unoccupied, the suitable habitat was fairly well saturated. They based their premise on the fact that, after some experience, it was possible to look ahead of the airplane and identify the lakes that would have swan broods present before the birds were in view. The "swan-type" water areas usually proved to have swans and the other types seldom did. The consistency of these observations would tend to reinforce the idea that little growth potential remains for Alaska's trumpeter swan population in much of its range.

Except on individual marshes or in other local situations, crowded habitat does not

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TABLE 19.—STRUCTURE OF ALASKA TRUMPETER SWAN POPULATION, 1968

	Paired Swans								
	Without Broods		With Broods		Cygnets[1]				
Area	No. of Prs.	% of Total Prs.	No. of Prs.	% of Total Prs.	No.	Avg. Brood Size	No. of Single Swans	No. of Swans in Flocks	Total No. of Swans
Kenai Peninsula	22	51.2	21	48.8	65	3.1	3	27	181
Cook Inlet–Susitna Basin	82	70.1	35	29.9	124	3.5	16	45	419
Gulkana Basin	92	63.9	52	36.1	190	3.6	31	81	590
Copper Canyon	17	58.6	12	41.4	44	3.7	3	53	158
Copper Delta–Gulf Coast	129	58.6	91	41.4	362	3.9	29	191	1,022
Tanana–Kantishna Valley	73	64.6	40	35.4	138	3.5	23	91	478
Total	415	62.3	251	37.7	923	3.6	105	488	2,848

[1] Two broods without adults present and 10 other broods accompanied by a single parent.

appear to be a limiting factor to the continued growth of the trumpeter swan population despite the impression of the observers that most of the optimum swan lakes were occupied. Approximately 3,500 swans in more than 22,000 square miles of waterfowl habitat should not constitute a "crowded" situation. A more likely explanation for the high ratio of nonproductive to productive pairs of swans in the Alaska population is their proximity to the northern limit of range. South of the 145-day ice-free line (Fig. 48) are many microclimates of less than 145 ice-free days during most years wherein successful production would not be possible even though mated pairs might be present there during a late summer survey. Marshes shielded from the moderating influence of the onshore spring winds off the Gulf of Alaska might remain frozen long enough to deny their use to nesting swans. Small changes in elevation produce disproportionately later changes in spring breakup as one progresses northward and inland compared to similar elevations in more southerly latitudes. Thus, much of the trumpeter swan range in Alaska may contain otherwise suitable habitat rendered unavailable at times due to geographic and weather conditions. Populations in the areas nearest the coast showed the highest ratio of productive pairs, although the margin was not great.

Under these circumstances, the structure of the trumpeter population in Alaska does not appear to give a valid measure of its growth potential at this time. Fortunately, a good departure point now exists from which to project changes as necessity or desirability to do so arises.

TRADITION AND THE POPULATION

Now that the future of the trumpeter swan as a species has been secured, what are the prospects for restoring it throughout its ancestral range and in its historic abundance?

Past

An understanding of this species' historic distribution and abundance, sketchy and incomplete at best, can only be speculated upon from a review of early records examined in light of recent investigations. It seems obvious now that the early arctic explorers, even though they apparently were able to distinguish between the 2 species of North American swans, made some errors in identification that have been perpetuated by subsequent ornithologists through citation of the original field records. Particularly suspect are alleged trumpeter swan sightings, unsupported by specimens, outside the current theoretical limit of range for this species but where the whistling swan is a common resident and the 2 could have been confused.

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A case in point is MacFarlane's (1891) records from the Canadian arctic coast. The area of his observations was ". . . bounded on the north by the Polar Sea . . . on the east by the coast of Franklin Bay from Cape Bathurst to its depth in Langton Harbor, on the west by the lower Mackenzie River, and on the south by the sixty-seventh parallel of north latitude . . . very few specimens indeed were gathered to the southward of 67°30'N and to the westward of longitude 129°, except from the lower Anderson to the Mackenzie." It was from here that MacFarlane reported: "Several nests of this species (*Olar buccinator*) were met with in the Barren Grounds, on islands in Franklin Bay, and one containing six eggs was situated near the beach on a sloping knoll. It was composed of a quantity of hay, down, and feathers intermixed, and this was the general mode of structure, of the nests of both swans." This is an excellent description of both the nest site and nest structure of the whistling swan but not of the trumpeter. Furthermore, the above area is from 150 to 200 miles beyond the theoretical limit of range of the trumpeter in a zone of only 120 to 130 ice-free days (Fig. 48).

This and other unsupported data from Adams (1878), Hearne (1795), and Swainson and Richardson (1832) was picked up by Baird, Brewer, and Ridgeway (1884) and woven routinely with accurate information into a dubious mosaic. For example, they stated that: "The trumpeter swan is exclusively found in the interior during the breeding season . . . It breeds in the interior as far north as the 70th parallel . . ." They stated further that the whistling swan ". . . is not, however, abundant on either coast near the sea. In the summer it frequents the high interior, and breeds on islands in inland lakes and along the shores of the Arctic Ocean." We know now that in the northern habitats, the whistling swan is a breeding resident of the coastal tundra whereas the trumpeter is oriented toward the boreal forests of the interior. Furthermore, it does not seem possible for the trumpeter to sustain a significant breeding population above 67° N latitude.

There is no reason to believe that, during the days of early exploration some 150 to 200 years ago, the climate would have allowed an annual ice-free period above 67° N latitude sufficient for successful trumpeter swan nesting. To the contrary, there seems to have been a northward advance of climate since the Pleistocene with a march of perhaps 75 miles a century taking place in recent history (Wing 1951). It seems certain therefore, that the trumpeters, then as now for the most part, were inland nesters whereas the whistlers were arctic coastal in origin. An exception could have been at the southeastern extreme of the trumpeters breeding range where the 145-day isopleth trends southerly across Hudson and James Bay.

In Alaska, historic distribution of the trumpeter swan can only be inferred despite a few scattered records, and knowledge of its abundance is more obscure than in Canada. Verification of the trumpeter swan as a nesting species near Ft. Yukon notwithstanding, there is little reason to believe that it was more abundant there in the early 19th century than at present. Alexander Murray established the Hudson's Bay Company fur trading post at Ft. Yukon in 1847. When Dall and Whymper first visited Ft. Yukon in July 1867 they made no mention of swan skins in the inventory (Mathews 1968). It seems highly unlikely that, if swans were readily available, the Hudson's Bay factor would not have acquired them at Ft. Yukon as assiduously as his counterparts did throughout Canada. Their absence in the fur trade at Ft. Yukon is indicative of their scarcity on the Yukon River drainage above Rampart as far as the Old Crow Flats and the Canadian border between Eagle and Dawson, the geographic area that supplied the Ft. Yukon fur trade.

William H. Dall (1870) is a source of further information concerning swans in the interior of Alaska. At Nulato where he had spent his first winter preparatory

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to a summer trip upriver to Ft. Yukon to take over the Hudson's Bay trading post for the United States, Dall stated that "On the 7th of May the first swans were seen. They are the small American species, the trumpeter not being found in this region, and very rarely visiting Ft. Yukon." Then on 27 May 1867, near the confluence of the Koyukuk River with the Yukon, Dall observed that "Swans, brant, and sandhill cranes were seen, the former abundantly." These observations conform to our present knowledge of range except that swans of neither species are abundant in that area. On the contrary they are quite scarce as breeding birds.

Farther upstream at a Russian trading post where the Tanana River joins the Yukon near the present village of Tanana, Dall made an observation of little more than social significance to him but which can now be interpreted in a different context. He described the Tanana River Indians mode of hair dressing as follows: "Allowed to grow to its full length, and parted in the middle, each lock was smeared with a mixture of grease and red ochre . . . The whole is then powdered with swan's-down, cut up finely, so that it adheres to the hair, presenting a most remarkable and singular appearance."

According to Dall the Tanana River Indians did not live in that immediate area, but came there periodically to trade at the Russian post from upriver in the vicinity of present-day Minto and Fairbanks. The "swan's-down" with which they decorated their hair would have come from trumpeters, the species that is breeding successfully in that same area now. No mention was made of the abundance of swans in the Tanana Valley, but there is no evidence that they were found in the Russian fur trade, either at that trading post or elsewhere.

In compiling statistics of the fur trade for 76 years in Alaska from Russian records, Dall (1870) did not mention swan skins although his list was complete enough to include ivory, whalebone, and castoreum in addition to all species of fur bearers both terrestrial and marine. In a detailed search of Russian records to determine the economic value and uses of swans in Alaska before United States acquisition of that territory in 1867, Banko (1962) concluded that swans did not figure in the early Alaskan fur trade to any significant degree, certainly not to the extent that they did in the Canadian fur trade where trumpeters were almost exterminated. It is interesting to note that the only swan record of commercial significance in Russian controlled Alaska involved the Hudson's Bay company. The records of the Russian–American Company, headquartered at Sitka, showed an offer (dated 1830–1831) from the Hudson's Bay Company to supply 130 swansdown vests for 6 shillings each (Banko 1962). The irony of this is that the vests offered to Russians in southeastern Alaska were undoubtedly manufactured from swans taken far to the east in the interior of North America, notwithstanding the fact that there was a flourishing market for Asiatic swan skins within Russia itself.

One might infer, based on the sparse observations of some of the early explorers, that the trumpeter swan was a more common breeding bird on the Yukon–Kuskokwim Delta and along the Bering Sea coast than elsewhere in Alaska. However, E. W. Nelson had a better perspective of swan distribution than other early observers. In reference to the trumpeter eggs collected near Ft. Yukon, Nelson (1887) stated that "There is no reason to suppose this swan ever reaches the shore of Bering Sea, where it appears to be entirely replaced by the other species. There is no (nesting) record of either bird being found on the southeastern coast of the Territory, where, however, both are likely to be found during the migrations."

Present

As we understand the current distribution of the 2 species of North American swans in relation to their ecological re-

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quirements, it seems obvious that the trumpeter could not have been more abundant historically on the fringe of its range near the Bering Sea than it is at present.

However, trumpeter swans are very likely more abundant now along the coast between Prince William Sound and the Yakutat area and in the lower Copper River Valley than they were during the early days of Alaskan exploration. This premise is based on the recent history of Alaskan glaciers as documented by Russian and other explorers and glaciologists since the mid-18th century (Tarr and Martin 1914). In commenting on glacial change, Flint (1947) stated that "Since the latter part of the nineteenth century glaciers all over the world, with local and temporary exceptions, have been shrinking. In some regions the shrinkage has been little short of catastrophic."

As recently as 1900, much of what is now optimum trumpeter swan nesting habitat in southern coastal Alaska was unsuitable moraine near the terminus of receding glaciers. Tarr and Martin (1914) noted that "Acres of moraine, too rocky for rapid growth of bushes, were still absolutely barren in 1910 . . ." This area that they described, formerly occupied by a southern protrusion of the Miles Glacier bulb, now provides several stable nesting territories for trumpeter swans. Some concept of the rate at which trumpeter swan habitat can be developed may be gained from the record of Abercrombie's explorations. In the 14-year period between his first and second trip on the lower Copper River, Abercrombie (1898) noted a dramatic change. In 1884, the faces of Miles and Childs glaciers protruded from opposite sides into the channel of the Copper River creating a series of impassable rapids which bear his name and are still impassable although considerably altered. By 1898, Miles Glacier had receded 5 to 6 miles from where the river washed its base 14 years earlier, leaving a wide expanse of lake and the "acres of moraine" described by Tarr and Martin.

Although such an exceptional rate of glacial decay has not been maintained, either with Miles Glacier or the several others in southern coastal Alaska, a general glacial recession has occurred within the past hundred years at least. Therefore, the current rate of population growth and trumpeter swan abundance in much of southcentral Alaska may well be a phenomenon of our times resulting from creation of habitat that was not available heretofore. Put another way, Alaska may have been a fringe area for the production of trumpeter swans in the historic past, in comparison to its major range in midcontinent, and the few records extant from Alaska could have represented a major contribution from the population present at the time.

Future

Perhaps the most we dare hope for the future of the trumpeter swan as well as for many other of Earth's threatened species is a partially satisfying "half-load" predicated upon the current man/environment relationship. Much of the type of environment required by the trumpeter swan, that is, specialized type of habitat, spacing needs among its own kind, insulation from human disturbance, has been irretrievably lost to man's interests and burgeoning numbers. This is particularly true in the food producing area extending from the prairie portion of the United States northward well into Canada's parkland and bush country. Through the transplanting program onto wildlife refuges and other sanctuaries that is currently underway and the natural spread of wild swans, induced by their own population pressure, the trumpeter swan most certainly can be restored to at least some of the historic range from which it was extirpated. In the remote northern areas with a sufficiently long ice-free period there should be little reason why this species cannot eventually be restored in considerable abundance.

A more optimistic future can only be prophesied in the hope that man will some-

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day supplant his self-dominant "superiority over beast" ethic with a visceral acceptance of his peer relationship to other creatures. As Henry Beston (1949) expressed this hope, "We need another and a wiser and perhaps a more mystical concept of animals. Remote from universal nature, and living by complicated artifice, man in civilization surveys the creature through the glass of his knowledge and sees thereby a feather magnified and the whole image in distortion. We patronize them for their incompleteness, for their tragic fate of having form so far below ourselves. And therein we err, and greatly err. For the animal shall not be measured by man. In a world older and more complete than ours they move finished and complete, gifted with extensions of the senses we have lost or never attained, living by voices we shall never hear. They are not brethren, they are not underlings; they are other nations caught with ourselves in the net of life and time, fellow prisoners of the splendor and travail of the earth."

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APPENDIX I

SUPPLEMENTAL DATA ON 117 TRUMPETER SWANS IN THE COPPER RIVER VALLEY, ALASKA, 1957–1959. ALL MEASUREMENTS ARE IN MILLIMETERS AND WEIGHTS TO THE NEAREST GRAM.

Number	Date	Sex	Age	Weight	Total length	Tarsus	Middle Toe	Claw	Wing	Number of tail feathers	Maximum tail feather length	Culmen length	Bill depth	Mandible	Nostril to nail	Nail length	Nail width
1	7/11/57	—	Cyg.	454	—	43.0	—	—	59.0	—	—	25.7	—	33.2	17.2	9.5	9.5
2	7/15/57	F	Cyg.	1588	—	80.6	—	—	113.2	—	—	41.3	—	50.4	24.3	12.0	11.5
3	7/15/57	F	Cyg.	1474	—	70.5	—	—	94.6	—	—	34.3	—	46.4	24.3	12.0	10.0
4	7/15/57	F	Cyg.	1531	—	75.5	—	—	113.0	—	—	40.7	—	50.4	24.9	—	—
5	7/16/57	F	Cyg.	1134	—	73.7	—	—	80.0	—	—	—	—	46.3	23.4	12.8	10.8
6	7/16/57	F	Cyg.	1077	—	70.0	—	—	88.0	—	—	36.9	—	45.7	23.4	9.9	10.0
7	7/16/57	M	Cyg.	1191	—	78.1	—	—	130.0	—	—	36.8	—	46.1	24.5	12.0	10.0
8	7/16/57	—	Cyg.	1077	—	73.2	—	—	100.0	—	—	35.8	—	44.7	24.0	12.0	10.0
9	7/16/57	F	Cyg.	1134	—	73.7	—	—	105.0	—	—	35.7	—	43.2	23.6	11.4	11.2
10	7/16/57	M	Cyg.	1134	—	72.8	—	—	120.0	—	—	36.5	—	45.3	24.4	12.7	11.1
11	7/16/57	F	Cyg.	454	—	51.5	—	—	71.5	—	—	31.2	—	38.0	20.5	9.3	10.0
12	7/16/57	F	Cyg.	510	—	52.5	—	—	70.0	—	—	30.8	—	39.2	19.4	9.0	10.6
13	7/21/57	M	Cyg.	227	—	47.0	—	—	52.2	—	—	23.2	14.0	30.0	14.1	10.0	10.5
14	8/2/57	M	Ad.	9525	—	160.0	—	—	2093.0	—	—	108.9	43.4	107.5	54.7	22.1	17.2
15	8/2/57	F	Ad.	9072	—	145.0	—	—	83.0	—	—	108.0	42.4	102.1	54.6	21.0	18.1
16	8/7/57	M	Cyg.	3062	—	111.5	—	—	180.0	—	—	51.3	28.0	73.0	31.5	17.8	14.2
17	8/7/57	M	Cyg.	2892	—	102.2	—	—	220.0	—	—	45.0	26.4	60.0	30.2	—	—
18	8/7/57	M	Cyg.	2948	—	109.0	—	—	220.0	—	—	50.0	30.2	63.9	31.0	16.5	15.0
19	8/7/57	—	Cyg.	3629	—	113.3	—	—	260.0	—	—	53.4	29.9	67.1	31.4	18.9	14.7
20	8/7/57	—	Cyg.	5443	—	125.0	—	—	500.0	—	—	62.8	33.3	—	40.0	16.6	14.9
21	8/7/57	—	Cyg.	6237	—	130.0	—	—	570.0	—	—	63.0	32.2	80.6	40.1	18.1	14.3
22	8/9/57	M	Cyg.	5443	1018.0	143.0	—	—	480.0	—	—	57.8	31.7	73.0	36.6	18.9	14.5
23	8/9/57	F	Cyg.	5387	—	143.0	—	—	480.0	—	—	56.7	34.0	73.9	38.6	17.9	15.5
24	8/9/57	F	Cyg.	4990	—	135.0	—	—	440.0	—	—	57.2	30.7	73.6	36.6	16.4	14.4
25	8/9/57	F	Cyg.	4423	—	130.0	—	—	390.0	—	—	54.8	28.7	70.0	35.8	15.3	14.9
26	8/9/57	M	Cyg.	4990	—	125.0	—	—	390.0	—	—	57.0	31.6	72.9	34.2	14.1	11.9
27	8/9/57	F	Cyg.	4876	—	130.0	—	—	400.0	—	—	59.5	31.9	73.9	35.4	14.4	13.2
28	8/9/57	F	Cyg.	3771	—	114.0	—	—	365.0	—	—	55.2	27.5	68.6	32.4	13.9	13.5
29	8/10/57	M	Cyg.	1474	580.0	78.9	—	—	150.0	—	—	41.3	22.0	50.5	25.6	12.0	11.4
30	8/10/57	M	Cyg.	1531	600.0	80.8	—	—	140.0	—	—	41.4	22.7	52.4	26.2	12.8	10.8
31	8/10/57	M	Cyg.	1531	590.0	78.0	—	—	150.0	—	—	42.8	23.7	51.3	26.2	12.0	12.0
32	8/11/57	M	Cyg.	4366	870.0	120.0	—	—	200.0	—	—	54.7	28.9	67.8	35.0	15.2	12.2
33	8/13/57	F	Cyg.	2325	750.0	91.9	—	—	200.0	—	—	48.8	28.5	57.9	29.5	12.3	12.3
34	8/13/57	F	Ad.	9299	1398.0	135.0	—	—	2039.0	—	—	112.5	42.1	103.0	54.3	21.5	19.6

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APPENDIX I (continued)

Number	Date	Sex	Age	Weight	Total length	Tarsus	Middle Toe	Claw	Wing	Number of tail feathers	Maximum tail feather length	Culmen length	Bill depth	Mandible	Nostril to nail	Nail length	Nail width
35	8/15/57	F	Cyg.	4990	950.0	125.0	—	—	460.0	—	—	58.6	35.3	76.6	39.6	15.7	14.9
36	8/17/57	M	Cyg.	5216	1060.0	140.0	—	—	460.0	—	—	59.9	34.9	74.0	35.5	17.0	14.2
37	8/17/57	F	Cyg.	4536	1050.0	133.0	—	—	380.0	—	—	59.5	35.0	75.8	35.2	17.8	14.6
38	8/17/57	F	Cyg.	4763	1050.0	125.0	—	—	410.0	—	—	57.3	34.4	74.3	34.7	17.0	14.9
39	8/17/57	F	Ad.	10,206	1442.0	152.5	—	—	—	—	—	120.0	46.0	114.3	—	21.3	18.6
40	6/22/58	F	Cyg.	340	—	49.7	45.0	8.5	75.0	—	—	26.4	16.5	34.1	18.2	10.2	9.8
41	6/22/58	M	Cyg.	340	—	47.9	44.6	8.7	75.0	—	—	26.0	16.1	32.2	17.9	11.2	9.4
42	6/22/58	F	Cyg.	340	—	48.4	47.3	8.9	80.0	—	—	27.2	15.4	33.0	17.7	9.4	8.1
43	6/22/58	F	Cyg.	312	—	49.9	44.0	8.3	80.0	—	—	27.1	16.2	33.5	18.6	10.1	11.8
44	6/23/58	F	Yrl.	8165	1320.0	116.2	132.0	20.0	—	21	180.0	99.9	42.1	100.8	56.9	14.4	16.7
45	6/26/58	F	Ad.	—	1450.0	115.0	140.0	25.0	2019.0	22	233.0	127.0	40.6	107.9	56.1	17.8	17.8
46	6/28/58	F	Ad.	10,433	1405.0	115.0	150.0	22.3	—	21	222.0	115.5	42.6	98.6	50.1	17.3	15.3
47	6/30/58	M	Yrl.	12,701	1400.0	125.0	152.0	27.0	—	21	210.0	132.0	44.2	111.1	55.6	22.8	18.2
48	7/1/58	M	Yrl.	11,793	1470.0	115.0	165.0	25.0	—	22	210.0	120.0	43.5	113.6	54.5	—	—
49	7/1/58	F	Yrl.	9979	1410.0	110.0	153.0	22.0	—	22	190.0	107.9	42.4	112.8	50.9	19.5	16.1
50	7/1/58	F	Yrl.	8618	1360.0	110.0	143.0	22.0	—	21	198.0	116.9	41.4	113.1	51.8	18.3	17.1
51	7/1/58	M	Yrl.	10,886	1430.0	125.0	160.0	24.0	—	23	190.0	113.4	41.2	114.7	53.2	18.2	16.2
52	7/3/58	M	Ad.	10,886	1445.0	116.0	160.0	25.0	—	22	231.0	117.3	40.5	107.8	56.2	21.5	19.8
53	7/4/58	M	Ad.	11,793	1578.0	115.0	160.1	21.9	—	22	234.0	123.0	42.9	107.3	56.8	23.7	19.5
54	7/7/58	F	Ad.	9072	1445.0	111.0	155.0	22.0	—	21	225.0	115.4	43.0	107.8	56.5	23.0	18.9
55	7/7/58	F	Ad.	9072	1450.0	114.0	145.0	23.0	2400.0	23	220.0	121.0	42.0	100.8	51.8	18.7	17.5
56	7/7/58	M	Ad.	10,886	1435.0	118.0	159.0	25.0	—	22	220.2	123.0	42.6	106.8	56.0	19.4	17.7
57	7/7/58	F	Yrl.	10,433	1402.0	112.0	145.0	22.0	—	22	—	—	—	—	—	—	—
58	7/7/58	M	Yrl.	12,247	1410.0	117.0	160.0	21.0	—	24	180.0	120.0	42.0	105.5	52.2	17.9	17.9
59	7/7/58	F	Yrl.	9525	1325.0	112.0	155.0	21.0	—	24	175.0	112.1	40.1	101.8	51.9	19.9	19.9
60	7/7/58	M	Yrl.	9979	1460.0	110.0	159.0	23.0	—	22	192.0	113.0	41.9	102.9	51.9	21.2	19.4
61	7/7/58	M	Yrl.	11,793	1405.0	110.0	165.0	23.0	—	—	—	114.9	42.2	114.3	52.6	21.0	19.1
62	7/7/58	M	Yrl.	10,886	1460.0	118.0	160.0	22.0	—	23	210.0	109.8	41.4	101.5	49.4	21.0	17.8
63	7/7/58	F	Yrl.	10,886	1440.0	113.0	155.0	21.0	—	23	195.0	106.9	41.9	99.9	50.1	19.4	17.0
64	7/7/58	F	Ad.	10,433	1475.0	111.0	169.0	25.0	—	22	215.0	115.7	40.2	102.1	51.5	19.9	18.9
65	7/7/58	M	Ad.	10,886	1430.0	120.0	156.0	26.0	—	20	—	129.0	42.4	109.1	55.0	21.5	21.0
66	8/2/58	M	Ad.	12,701	1535.0	116.0	172.0	28.0	—	—	205.0	116.4	41.9	109.3	57.9	26.0	20.0
67	8/4/58	M	Cyg.	6350	1250.0	92.0	140.0	17.0	—	22	125.0	63.6	35.4	79.1	39.9	18.7	14.9
68	8/4/58	F	Cyg.	5897	1195.0	95.0	140.0	17.0	—	22	130.0	70.9	34.7	83.2	43.7	19.0	15.0
69	8/4/58	F	Cyg.	6577	1205.0	88.0	140.0	16.0	—	20	140.0	69.9	37.0	84.9	41.1	20.6	15.9
70	8/4/58	M	Ad.	13,608	1495.0	118.0	167.0	29.0	—	22	212.0	125.0	45.3	113.1	58.3	22.3	19.4

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APPENDIX I (continued)

Number	Date	Sex	Age	Weight	Total length	Tarsus	Middle Toe	Claw	Wing	Number of tail feathers	Maximum tail feather length	Culmen length	Bill depth	Mandible	Nostril to nail	Nail length	Nail width
71	8/4/58	—	Cyg.	7257	1200.0	94.4	135.0	18.0	—	22	135.0	66.0	38.4	83.2	40.1	19.7	15.0
72	8/5/58	M	Yrl.	10,886	1420.0	108.0	155.0	24.0	2188.0	22	210.0	118.0	42.3	109.0	56.2	23.0	19.6
73	8/5/58	F	Yrl.	10,886	1420.0	106.0	157.0	24.0	2244.0	22	210.0	110.3	41.1	101.6	50.7	22.5	19.8
74	8/6/58	M	Ad.	13,154	1425.0	112.0	155.0	28.0	—	22	210.0	116.0	42.4	106.2	56.5	22.2	18.3
75	8/6/58	—	Cyg.	7031	1220.0	105.0	145.0	17.0	—	23	150.0	69.4	32.1	86.6	45.3	20.5	15.6
76	8/6/58	F	Cyg.	6804	1190.0	92.0	135.0	17.0	—	21	135.0	66.5	37.8	81.6	40.0	18.6	15.0
77	8/6/58	M	Cyg.	7484	1195.0	95.0	135.0	18.0	—	21	135.0	64.0	41.2	83.3	41.3	18.7	14.3
78	8/6/58	M	Cyg.	8618	1260.0	105.0	155.0	21.0	—	22	150.0	71.4	41.6	92.6	46.0	19.8	14.6
79	8/6/58	F	Cyg.	7257	1235.0	110.0	150.0	19.0	—	20	145.0	66.8	37.8	86.1	42.2	22.5	14.8
80	8/6/58	F	Cyg.	7711	1205.0	108.0	145.0	19.0	—	21	150.0	68.9	38.7	88.4	44.4	21.3	14.0
81	8/6/58	M	Cyg.	7257	1180.0	104.0	136.0	18.0	—	21	135.0	63.6	37.3	84.0	41.2	18.5	14.0
82	8/6/58	M	Cyg.	7938	1240.0	110.0	145.0	20.0	—	21	150.0	70.0	41.1	88.5	43.4	22.2	19.1
83	8/26/58	M	Cyg.	—	—	100.0	150.0	19.0	1560.0	21	125.0	69.3	39.7	82.2	41.6	20.8	15.0
84	6/15/59	M	Ad.	—	—	120.0	170.0	24.0	—	22	—	122.0	54.6	115.5	60.2	—	—
85	6/27/59	M	Cyg.	—	—	41.0	48.3	9.1	—	—	—	28.5	27.9	36.5	18.1	—	—
86	6/27/59	F	Cyg.	—	—	40.6	47.8	8.2	—	—	—	27.1	26.7	34.8	16.9	—	—
87	6/27/59	M	Cyg.	—	—	41.6	48.1	8.3	—	—	—	29.1	27.5	36.2	18.1	—	—
88	6/27/59	F	Cyg.	—	—	38.1	46.8	9.1	—	—	—	29.1	27.5	36.2	17.4	—	—
89	6/27/59	M	Ad.	12,701	—	112.0	155.0	27.0	—	22	210.0	116.5	41.7	115.7	57.1	23.4	17.8
90	6/27/59	M	Ad.	—	—	115.0	163.0	24.0	—	22	228.0	131.0	47.7	113.4	57.3	—	—
91	7/11/59	M	Cyg.	—	—	34.4	41.4	7.8	—	—	—	25.4	14.1	29.8	15.7	9.2	9.2
92	7/11/59	F	Cyg.	—	—	35.8	42.9	8.3	—	—	—	24.2	13.8	229.5	15.3	9.1	9.1
93	7/11/59	M	Cyg.	—	—	36.4	39.8	8.3	—	—	—	23.5	13.9	29.8	15.5	9.5	9.5
94	7/5/59	M	Ad.	—	—	105.0	155.0	24.0	—	21	205.0	111.8	41.0	113.7	52.5	18.7	16.8
95	7/5/59	F	Cyg.	—	—	38.1	45.1	7.9	—	—	—	26.9	15.5	32.8	17.8	—	—
96	7/11/59	M	Cyg.	—	—	39.0	44.2	8.5	—	—	—	28.8	17.3	34.8	19.9	9.9	9.9
97	7/27/59	F	Ad.	9525	—	110.0	163.0	23.0	—	22	190.0	119.9	41.7	108.6	55.0	—	—
98	7/27/59	M	Ad.	13,608	—	120.0	163.0	27.0	—	22	224.0	125.0	45.8	113.6	57.9	—	—
99	7/31/59	F	Ad.	9525	—	110.0	160.0	23.0	—	24	215.0	111.2	40.5	101.9	50.4	20.5	15.4
100	7/31/59	F	Cyg.	2495	—	65.4	78.2	9.5	—	—	—	49.2	27.4	55.7	27.6	13.9	10.2
101	8/2/59	M	Cyg.	5216	—	92.9	125.0	15.0	—	—	—	62.9	37.3	74.8	35.4	—	—
102	8/5/59	F	Ad.	9752	—	110.0	145.0	24.0	—	20	190.0	115.1	42.1	116.1	53.6	22.2	17.5
103	8/5/59	M	Cyg.	2722	—	64.5	77.3	9.8	—	—	—	48.5	27.9	57.1	30.2	13.8	11.5
104	8/5/59	M	Cyg.	2495	—	63.0	79.2	10.3	—	—	—	47.9	27.3	56.5	29.1	14.4	12.5
105	8/6/59	F	Cyg.	3742	—	83.3	108.8	12.5	—	—	—	64.2	31.6	63.5	31.4	13.2	12.4

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APPENDIX I (continued)

Number	Date	Sex	Age	Weight	Total length	Tarsus	Middle Toe	Claw	Wing	Number of tail feathers	Maximum tail feather length	Culmen length	Bill depth	Mandible	Nostril to nail	Nail length	Nail width
106	8/6/59	F	Cyg.	3969	—	78.5	112.4	12.5	—	—	—	59.4	32.4	64.8	31.0	15.0	11.9
107	8/6/59	F	Cyg.	3742	—	75.5	101.0	11.8	—	—	—	61.1	32.1	62.7	30.0	12.7	12.1
108	8/7/59	M	Cyg.	2495	—	64.2	79.8	10.1	—	—	—	50.2	26.7	57.7	28.8	14.3	11.3
109	8/7/59	M	Cyg.	2835	—	71.2	78.1	10.9	—	—	—	53.1	31.0	58.4	30.8	15.1	11.8
110	8/8/59	F	Yrl.	7711	1370.0	110.0	155.0	20.0	2222.0	—	—	113.6	43.3	107.3	54.9	22.1	17.8
111	8/8/59	F	S. Ad.	8391	1345.0	112.0	150.0	20.0	2263.0	—	—	112.7	39.8	111.4	53.3	19.7	18.4
112	8/8/59	F	Ad.	9525	1420.0	107.0	160.0	25.0	2175.0	—	—	111.0	42.3	100.8	50.7	19.8	17.5
113	8/10/59	M	Cyg.	—	—	81.9	110.4	12.7	—	—	—	76.4	36.1	69.7	36.9	16.5	13.0
114	8/10/59	F	Cyg.	4309	—	81.7	101.6	12.0	—	—	—	70.1	33.0	69.5	35.0	14.8	14.0
115	8/10/59	F	Cyg.	4423	—	91.3	107.6	12.3	—	—	—	71.3	34.5	69.8	35.0	15.0	13.2
116	8/10/59	M	Cyg.	1588	—	52.5	60.4	9.6	—	—	—	41.5	25.8	50.8	27.0	12.3	11.0
117	8/10/59	M	Cyg.	1871	—	57.9	64.5	9.0	—	—	—	45.8	28.2	52.4	27.0	12.1	10.6

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APPENDIX II

MEASUREMENTS OF TRUMPETER SWAN EGGS IN ALASKA, 1957–1959

Year and Clutch No.	Egg No.	Length (mm)	Width (mm)	Weight (g)
1957—1	1[a]	113.1	71.3[a]	281
2	1[a]	113.3	72.7[a]	288
3	1[a]	117.6	77.8[a]	339
	2	123.0	78.0	—
	3	122.0	81.0	—
	4	120.0	79.0	—
	5	122.0	80.0	—
4	1	115.4	72.0	—
	2	117.6	74.0	—
	3[b]	117.8	73.7[b]	—
	4	118.3	74.8	—
5	1	121.7	76.4	—
	2	119.5	75.6	—
	3	121.2	77.2	—
	4	121.3	76.3	—
	5	120.8	77.3	—
6	1	116.6	78.3	—
	2	117.5	78.2	—
	3	114.5	78.3	—
	4	113.2	77.4	—
	5	113.8	77.5	—
	6	114.4	77.2	—
	7	116.3	78.2	—
1958—1[c]	1	119.0	73.0	—
	2	118.0	73.0	—
2[c]	1	120.0	75.0	—
3	1	111.7	74.9	—
	2	112.0	73.9	—
	3	112.5	74.2	—
	4	109.8	72.0	—
4	1	121.0	76.3	—
	2	124.0	76.4	—
	3	122.0	76.2	—
	4	119.0	76.0	—
	5	123.0	75.4	—
5[c]	1	119.6	79.1	—
	2	120.5	78.2	—
	3	115.1	79.3	—
6[c]	1	117.4	74.2	—
1959—1	1	117.0	70.0	—
	2	117.1	73.9	—
2	1	110.0	74.6	—
	2	110.9	74.7	—
3	1	117.9	76.8	400
	2	117.9	76.1	390
	3	114.5	75.7	375
	4	116.5	76.2	375
	5	117.5	76.1	375
4[c]	1	113.9	76.3	—
	2	114.0	76.5	—
5	1	115.0	70.9	350
	2	112.8	73.7	350
	3	115.7	74.2	350
	4	111.2	73.8	350
6	1	117.8	74.2	350
	2	115.7	73.7	350
	3	113.9	73.4	340
	4	115.5	75.2	350
	5	118.6	74.3	350
	6	114.9	74.7	350
7	1	120.0	75.2	360
	2	122.0	76.8	400
	3	118.2	74.0	375
	4	114.6	76.3	375
	5	112.4	75.5	350
8	1	118.0	76.2	390
	2	122.0	74.3	390
	3	112.2	75.2	350
	4	114.6	76.9	390
	5	119.0	76.2	395
	6	117.5	76.5	395
9	1	120.0	76.9	375
	2	117.3	75.3	390
	3	117.1	75.3	360
	4	120.0	74.9	375
	5	118.0	75.8	375
10	1	112.0	72.0	325
	2	114.5	73.0	350
	3	112.0	71.9	325
	4	111.8	73.2	350
	5	111.5	73.5	350
11	1	114.0	71.9	325
	2	123.0	73.6	375
	3	123.0	73.3	350
	4	124.0	70.5	350
12	1	125.0	72.4	350
	2	123.0	73.6	350
	3	123.0	73.6	350
	4	122.0	72.7	350
13	1	112.3	73.4	325
	2	112.1	72.8	325
	3	112.0	72.8	300
	4	111.2	72.0	300
14	1	114.2	75.9	350
	2	114.5	75.2	350
	3	112.5	73.4	340
	4	114.1	75.2	350
	5	113.9	75.5	350
15	1	120.0	74.3	375
	2	121.0	74.6	375
	3	119.3	74.3	375
	4	121.0	73.3	375
	5	117.8	72.9	350

[a] Abandoned eggs.
[b] Egg was collected and forwarded to the U. S. National Museum, Wash., D. C.
[c] Incomplete clutch.

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APPENDIX II (Continued)

Year and Clutch No.	Egg No.	Length (mm)	Width (mm)	Weight (g)	Year and Clutch No.	Egg. No.	Length (mm)	Width (mm)	Weight (g)
16	1	113.9	72.0	325		3	120.0	74.9	390
	2	110.7	73.4	315		4	115.0	74.4	375
	3	110.6	72.0	310		5	117.5	77.3	390
	4	110.9	73.7	300	21	1	122.0	75.0	390
	5	109.8	69.8	300		2	123.0	74.4	375
	6	110.9	73.7	310		3	122.0	74.7	380
17	1	114.4	74.3	350	22	1	125.0	76.0	410
	2	116.0	74.5	380		2	124.0	72.5	390
	3	117.3	74.2	360		3	123.0	73.6	395
18	1	119.5	77.8	400		4	123.0	75.0	400
	2	122.0	76.2	400		5	121.0	75.0	375
	3	117.0	77.3	380	23	1	119.0	77.0	400
	4	123.0	76.4	400		2	116.0	76.7	390
	5	117.9	77.5	400		3	112.7	78.0	390
	6	118.7	76.7	390		4	115.1	77.3	390
	7	118.3	77.9	400	24	1	116.4	74.9	360
19	1	123.0	76.5	390		2	121.0	75.2	390
	2	120.0	75.3	380		3	118.5	74.1	350
	3	124.0	75.6	400		4	120.5	73.8	360
	4	124.5	74.5	385		5	117.0	73.9	350
20	1	117.0	76.7	390		6	121.0	75.0	360
	2	119.1	75.3	390					

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APPENDIX III

SUMMARY OF PLANT TRANSECTS BY COMMUNITIES, BREMNER RIVER, ALASKA

	Potamogeton		*Hippuris/Sparganium*													
Pond number	4	PL	4	7	4	4	6	6	4	4	4	4	4	4	4	4
Pond type	P	L	P	RS	P	P	BP	BP	P	P	P	P	P	P	P	P
Water depth, in.	36	24	30	36	30	30	36	36	30	30	30	30	30	30	30	30
Turbidity	C	C	C	C	C	C	.3	.3	C	C	C	C	C	C	C	C
pH open water	7.1	—	7.1	7.1	7.1	7.1	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.0
pH at stand	7.1	—	—	—	—	—	—	—	6.8	6.8	6.8	6.8	6.8	6.8	6.8	6.8
Av. depth	1.6	—	1.6	1.1	1.6	1.6	—	—	1.6	1.6	1.6	1.6	1.6	1.6	1.6	1.6
Water stability	S	SF	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Bottom	SD	HS	SD	SD	SD	SD	SD	SD	SD	SD	SD	SD	SD	SD	SD	SD
Percentage emergents	86	—	86	94	86	86	—	—	86	86	86	86	86	86	86	86
Transect number	11	2	8	31	10	9	73	74	56	57	58	59	60	53	54	55
Equisetum f.	—	—	2	26	—	—	—	—	—	—	—	—	—	—	—	—
Potamogeton p. r.	100	—	22	24	—	—	—	—	24	28	52	52	54	36	42	38
Potamogeton p.	—	96	—	—	—	—	—	—	—	—	—	—	—	26	26	18
Hippuris v.	—	—	100	100	18	14	76	90	96	98	100	100	100	—	—	—
Sparganium a.	—	—	24	16	80	98	—	—	26	40	62	64	56	98	96	100
Utricularia m.	—	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Glyceria sp.	—	—	—	—	44	—	—	—	—	—	—	—	—	—	—	—
Callitriche h.	—	2	—	—	—	—	—	—	—	—	—	—	—	10	—	—

Key:

PA = peninsula lake
P = pond
L = lake
RS = river scour
BP = beaver pond

.3 = secchi reading in meters
C = clear
S = stable
SF = some fluctuation
VF = violent fluctuation

SD = sand
HS = hard sand
GS = glacial silt
VG = decayed vegetation

	Equisetum															
Pond number	4	4	7A	7	7	6	4	1	4	4	4	4	4	4	4	4
Pond type	P	P	RS	RS	RS	BP	P	RS	P	P	P	P	P	P	P	P
Water depth, in.	18	18	—	24	18	24	18	30	18	18	18	18	18	18	18	18
Turbidity	C	C	C	C	C	.3	C	C	C	C	C	C	C	C	C	C
pH open water	7.1	7.1	7.3	7.0	7.0	7.0	7.1	8.4	7.1	7.1	7.1	7.1	7.1	7.1	7.1	7.1
pH at stand	—	—	—	—	—	—	—	6.8	6.2	6.2	6.2	6.2	6.2	6.2	6.2	6.2
Av. depth	1.6	1.6	2.5	1.1	1.1	—	1.6	—	1.6	1.6	1.6	1.6	1.6	1.6	1.6	1.6
Water stability	S	S	VF	S	S	S	S	S	S	S	S	S	S	S	S	S
Bottom	SD	SD	SD	SD	SD	GS	SD	VG	HS	HS	HS	SD	SD	SD	SD	SD
Percentage emergents	86	86	1	74	74	—	86	—	86	86	86	86	86	86	86	86
Transect number	6	.7	40	28	32	16	12	46	50	51	52	61	62	63	64	65
Equisetum f.	100	100	100	100	100	100	100	90	100	100	100	100	100	100	100	100
Potamogeton p. r.	22	24	—	—	—	—	—	30	28	20	12	18	8	10	8	8
Potamogeton p.	—	—	—	—	—	—	—	14	2	6	4	—	—	—	—	—
Hippuris v.	52	32	—	—	—	—	—	26	6	—	—	6	4	32	10	22
Sparganium	24	16	—	—	4	—	—	—	2	10	8	24	18	22	26	58
Potentilla p.	—	—	—	—	—	12	—	—	—	—	—	—	—	—	—	—
Moss	—	—	—	—	—	—	—	12	—	—	—	—	6	8	—	—
Utricularia m.	—	—	—	—	8	10	—	—	2	6	—	24	20	10	—	12
Carex a.	—	—	—	—	12	2	—	—	—	—	—	—	—	—	—	—
Carex r.	—	—	—	—	—	—	—	6	—	—	—	—	—	—	—	—

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APPENDIX III (Continued)

	Equisetum (Continued)			*Equisetum/Potentilla*/Moss											
Pond number	4	4	7B	7	10	7	10	6	8	8	6	6	6	6	8
Pond type	P	P	RS	RS	BP	RS	BP	BP	BP	BP	BP	BP	BP	BP	BP
Water depth, in.	18	18	18	18	18	18	18	18	12	12	24	24	24	24	18
Turbidity	C	C	C	C	.35	C	.35	.30	.15	.15	.30	.30	.30	.30	.15
pH open water	7.1	7.1	7.0	7.0	7.1	7.0	7.1	7.0	6.9	6.8	7.0	7.0	7.0	7.0	6.9
pH at stand	6.2	6.2	—	—	—	—	—	6.8	—	5.4	6.8	6.8	6.8	6.8	—
Av. depth	1.6	1.6	—	—	—	1.1	—	—	1.8	1.8	—	—	—	—	1.8
Water stability	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Bottom	SD	SD	SD	SD	GS	SD	GS	GS	GS	GS	GS	GS	GS	GS	GS
Percentage emergents	86	86	86	—	—	74	—	—	.06	.06	—	—	—	—	.06
Transect number	66	67	80	35	27	30	25	15	22	42	69	70	71	72	41
Equisetum f.	100	100	100	100	100	100	88	100	62	100	90	100	90	100	100
Potamogeton p. r.	2	20	—	—	—	—	—	—	—	—	—	—	—	—	—
Hippuris v.	20	14	28	10	4	18	—	—	—	—	4	—	4	—	—
Sparganium q.	48	32	—	4	2	4	—	—	—	—	—	—	—	—	—
Potentilla p.	—	—	—	—	—	—	2	80	92	100	84	86	70	74	100
Moss	—	—	—	92	100	48	10	20	—	42	96	76	100	80	100
Utricularia m.	8	8	—	—	—	44	—	—	—	—	6	8	—	4	—
Carex a.	—	—	—	—	10	20	78	2	—	10	—	—	2	4	4

	Carex/Equisetum									*Carex/Potentilla*/Moss							
Pond number	PL	PL	PL	7A	7B	9	9	9	10	1	6	7B	1	1	1	1	1
Pond type	L	L	L	RS	RS	BP	BP	BP	BP	RS	BP	RS	RS	RS	RS	RS	RS
Water depth, in.	4	4	8	8	12	12	18	12	18	6	12	12	3	6	0	3	3
Turbidity	C	C	C	C	C	.25	.25	.25	.35	C	.30	C	C	C	C	C	C
pH open water	—	—	—	7.3	7.0	7.0	7.0	7.0	7.1	8.4	7.0	7.0	8.4	8.4	8.4	8.4	8.4
pH at stand	—	—	—	—	—	—	—	—	—	—	6.8	—	—	6.8	5.2	5.2	6.8
Av. depth	—	—	—	2.5	—	2.6	2.6	2.6	—	—	—	—	—	—	—	—	—
Water stability	SF	SF	SF	VF	S	S	S	S	S	S	S	S	S	S	S	S	S
Bottom	HS	HS	HS	S	SD	GS	GS	GS	GS	SD	GS	SD	VG	VG	VG	VG	VG
Percentage emergents	—	—	—	1	—	.08	.08	.08	—	—	—	—	—	—	—	—	—
Transect number	3	4	5	39	33	17	18	19	26	1	14	34	78	47	48	49	45
Equisetum f.	18	4	—	16	68	14	46	28	41	32	10	8	32	28	—	—	62
Hippuris v.	—	2	10	—	—	—	—	—	—	—	—	6	—	—	—	—	10
Sparganium q.	—	—	—	—	—	—	—	—	—	—	—	10	—	—	—	—	—
Potentilla p.	—	—	—	—	12	—	—	—	—	36	90	48	18	72	24	28	44
Moss	—	—	—	—	2	—	—	—	—	10	—	—	100	52	100	100	38
Utricularia m.	34	22	10	—	8	—	—	—	—	—	—	—	—	—	—	—	—
Carex a.	2	—	4	—	100	80	84	62	94	72	78	92	—	24	—	—	34
Carex r.	100	100	100	98	—	24	10	48	14	—	—	—	90	80	100	6	72
Calamagrostis c.	—	—	—	—	—	2	—	—	—	—	—	—	2	—	—	—	—
Glyceria sp.	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
Menyanthes t.	—	—	—	46	—	—	—	—	—	—	—	—	—	—	—	—	—
Eriophorum a.	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
Juncus m.	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

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APPENDIX III (Continued)

	Carex-Salix/Moss				*Calamagrostis-Salix/Equisetum*					*Glyceria*				
Pond number	7	7	4	7	6	6	6	1	8	8	8	8	8	8
Pond type	RS	RS	P	RS	BP	BP	BP	RS	BP	BP	BP	BP	BP	BP
Water depth, in.	1	1	3	0	0	0	0	0	0	4	4	4	4	4
Turbidity	C	C	C	C	.30	.30	.30	.30	.15	.15	.15	.15	.15	.15
pH open water	7.0	7.0	7.1	7.0	7.0	7.0	7.0	6.8	6.9	6.8	6.8	6.9	6.9	6.9
pH at stand	5.8	5.8	—	—	6.0	6.0	6.0	5.2	—	5.4	5.4	—	—	—
Av. depth	1.1	1.1	1.6	—	—	—	—	—	1.8	1.8	1.8	1.8	1.8	1.8
Water stability	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Bottom	VG	VG	S	VG	GS	GS	GS	VG	GS	GS	GS	GS	GS	GS
Percentage emergents	74	74	86	74	—	—	—	—	.06	6	6	6	6	6
Transect number	81	68	13	29	75	76	77	50	24	42	44	23	20	21
Equisetum f.	32	—	14	—	4	22	22	—	—	6	8	2	—	4
Equisetum a.	—	20	18	—	92	58	80	86	—	—	—	—	—	—
Hippuris v.	—	—	—	—	—	—	—	—	—	12	6	—	8	—
Potentilla p.	4	—	6	28	42	—	28	84	—	32	4	100	4	4
Moss	100	100	—	—	—	—	—	86	—	—	—	—	—	—
Carex a.	2	—	—	—	—	—	—	—	—	60	—	—	—	96
Carex r.	—	—	—	—	—	—	—	2	—	—	—	—	—	—
Carex spp.	83	96	100	100	32	34	22	—	—	—	—	—	—	—
Salix spp.	46	20	—	—	—	—	18	34	—	2	—	—	—	—
Calamagrostis c.	4	—	—	—	98	100	100	—	100	8	—	—	—	—
Glyceria sp.	—	—	—	—	—	—	—	—	—	72	100	70	100	60

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APPENDIX IV

LIST OF BIRDS AND MAMMALS ASSOCIATED WITH THE TRUMPETER SWAN HABITAT IN THE LOWER COPPER RIVER VALLEY OF ALASKA

Nomenclature based on AOU checklist of North American Birds, 5th ed., and on G. S. Miller and R. Kellog List of North American Recent Mammals, U.S. Natl. Mus. Bull. 205. 1955.

Birds
Gavia immer, Common loon
Gavia stellata, Red-throated loon
Podiceps auritus, Horned grebe
Olor columbianus, Whistling swan
Olor buccinator, Trumpeter swan
Branta canadensis occidentalis, Canada goose
Anas platyrhynchos, Mallard
Anas strepera, Gadwall
Anas acuta, Pintail
Anas carolinensis, Green-winged teal
Anas discors, Blue-winged teal
Mareca americana, American widgeon
Spatula clypeata, Shoveler
Aythya americana, Redhead
Aythya valisineria, Canvasback
Aythya marila, Greater scaup
Bucephala clangula, Common goldeneye
Bucephala islandica, Barrow's goldeneye
Bucephala albeola, Bufflehead
Histrionicus histrionicus, Harlequin duck
Mergus serrator, Red-breasted merganser
Haliaeetus leucocephalus, Bald eagle
Pandion haliaetus, Osprey
Falco peregrinus, Peregrine falcon
Lagopus lagopus, Willow ptarmigan
Charadrius semipalmatus, Semipalmated plover
Capella gallinago, Common snipe
Numenius phaeopus, Whimbrel
Actitis macularia, Spotted sandpiper
Tringa solitaria, Solitary sandpiper
Totanus flavipes, Lesser yellowlegs
Erolia minutilla, Least sandpiper
Limnodromus griseus, Short-billed dowitcher
Ereunetes pusillus, Semipalmated sandpiper

APPENDIX IV (continued)

Birds
Lobipes lobatus, Northern phalarope
Larus hyperboreus, Glaucous gull
Larus canus, Mew gull
Sterna paradisaea, Arctic tern
Asio flammeus, Short-eared owl
Megaceryle alcyon, Belted kingfisher
Empidonax spp., Flycatcher
Tachycineta thalassina, Violet-green swallow
Iridoprocne bicolor, Tree swallow
Perisoreus canadensis, Gray jay
Pica pica, Black-billed magpie
Corvus corax, Common raven
Hylocichla guttata, Hermit thrush
Lanius excubitor, Northern shrike
Seiurus noveboracensis, Northern waterthrush
Agelaius phoeniceus, Red-winged blackbird
Euphagus carolinus, Rusty blackbird
Passerculus sandwichensis, Savannah sparrow
Passerella iliaca, Fox sparrow

Mammals
Sorex spp., Shrew
Myotis lucifugus, Little brown bat
Lepus americanus, Varying hare
Castor canadensis, Beaver
Synaptomys borealis, Bog lemming
Clethrionomys rutilus, Red-backed mouse
Microtus oeconomus, Tundra vole
Ondatra zibethica, Muskrat
Erethizon doreatum, Porcupine
Canis latrans, Coyote
Canis lupus, Wolf
Vulpes fulva, Red fox
Euarctos americanus, Black bear
Ursus sp., Brown bear
Martes americana, Marten
Mustela erminea, Short-tailed weasel
Mustela vison, Mink
Gulo luscus, Wolverine
Lutra canadensis, Land otter
Alces alces, Moose

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APPENDIX V

A LIST OF PLANTS COLLECTED IN THE TRUMPETER SWAN HABITAT OF THE LOWER COPPER RIVER VALLEY OF ALASKA, 1957–1959, AND DEPOSITED IN THE WASHINGTON STATE UNIVERSITY AND UNIVERSITY OF ALASKA HERBARIUMS

Pteridium aquilinum, Western bracken
Equisetum arvense, Common horsetail
Equisetum fluviatile, Swamp horsetail
Equisetum hiemale var. *californicum*, Scouring-rush
Chamaecyparis nootkatonsis, Yellow cedar
Larix laricina, Tamarack
Abies lasiocarpa, Alpine fir
Tsuga heterophylla, Western hemlock
Tsuga mertensiana, Mountain hemlock
Picea mariana, Black spruce
Picea glauca, White spruce
Picea sitchensis, Sitka spruce
Sparganium angustifolium, Narrow-leaved burreed
Sparganium minimum, Small burreed
Potamogeton alpinus, Northern pondweed
Potamogeton perfoliatus var. *richardsonii*, Clasping-leaved pondweed
Potamogeton pectinatus, Fennel-leaved pondweed
Calamagrostis canadensis, Bluejoint
Glyceria sp., Mannagrass
Eleocharis palustris, Creeping spikerush
Eriophorum scheuchzeri, White cotton-grass
Eriophorum angustifolium, Tall cotton-grass
Scirpus pacificus, Pacific bulrush
Scirpus microcarpus, Small-fruited bulrush
Scirpus validus, Great bulrush
Carex aquatilis, Water sedge
Carex mertensii, Mertens sedge

APPENDIX V (continued)

Carex livida, Livid sedge
Carex rostrata, Beaked sedge
Lemna trisulca, Ivy-leaved duckweed
Lemna minor, Lesser duckweed
Juncus triglumis, Three-flowered rush
Juncus mertensianus, Mertens rush
Populus tremuloides, Quaking aspen
Populus tacamahacca, Balsam poplar
Populus tricocarpa, Black cottonwood
Salix spp., Willow
Myrica gale, Sweet gale
Betula papyrifera, Western paper birch
Alnus crispa, Green alder
Urtica lyallii, Lyall nettle
Ranunculus aquatilis, White water-crowfoot
Nuphar polysepalum, Yellow pond lily
Nymphaea tetragona, White water lily
Spirea sp., Spirea
Rubus spp., Raspberry
Rosa sp., Rose
Potentilla palustris, Marsh cinquefoil
Callitriche autumnalis, Northern water-starwort
Lupinus nootkatensis, Nootka lupine
Epilobium angustifolium, Fireweed
Epilobium latifolium, Riverweed
Myriophyllum sp., Water milfoil
Hippuris vulgaris, Common mare's tail
Oplapanax horridus, Devil's Club
Chamaedaphne calyculata, Leatherleaf
Vaccinium spp., Blueberry
Menyanthes trifoliata, Buckbean
Utricularia macrorhiza, Common bladderwort
Sambucus racemosa, Red-berried elder
Viburnum edule, Highbush cranberry

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