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The ecology of trumpeter swan in Yellowstone National Park and vicinity

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THE ECOLOGY OF TRUMPETER SWAN IN YELLOWSTONE NATIONAL PARK AND VICINITY

By

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Trumpeter Swans in the vicinity of Yellowstone National Park, Wyoming, were studied from September 1976 to April 1979. Thirty nesting pairs fledged 0.44 cygnets per active nest. Clutch size averaged 4.21 eggs. The hatching rate of eggs was 49%; nesting success was 71% in 1977 and 41% in 1978.

Swans with above average clutches incubated with higher constancy, longer sessions, shorter recesses, and fewer recesses per day than swans with below average clutches. Cygnets from large clutches suffered significantly lower mortality than those from clutches of four eggs or fewer.

Pre-fledging cygnet mortality totaled 76% of the 87 cygnets. Of the cygnets that lived to September, 22% were retarded in development. Moribund cygnets showed extreme weakness, leg and foot deformities, and rapid flicking of the head.

Human activity made three historic territories in YNP unsuitable for nesting. Human activity at 14 other territories did not decrease the success of active nests but reduced the number of nesting attempts.

Migratory Canadian Trumpeters arrived after 15 October and remained from 3 to 12 weeks on Yellowstone Lake before continuing southwest to the Snake River Drainage in Idaho. Up to 468 Trumpeters used Yellowstone Lake and between 500 and 600 wintered at Harriman State Park. Increasing human activity will continue to force swans from peripheral wintering sites into these few remaining secluded areas.

The recent reproductive failure of Trumpeters in YNP and the slow decline in the regional adult population since 1964 are continuing. Increased competition on limited wintering habitat may leave many breeding swans in poor condition and decrease the number and viability of their offspring. Dispersal of the wintering Trumpeters is necessary to reduce the population's present vulnerability to disease and competition.

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CHAPTER I

INTRODUCTION

Current Status and Distribution

The Trumpeter Swan (Cygnus buccinator) is the largest member of the family Anatidae and one of the rarest North American waterfowl species. Approximately 5000 Trumpeters currently exist in the wild. The Pacific population of about 4150 (Trumpeter Swan Society 1976) breeds in Alaska and winters along the coast from Alaska south to Washington and at a few isolated lakes in British Columbia. The midcontinental population of approximately 750 adults and their offspring (USFWS Swan Survey 1979) winters in the Tri-state Region of Montana, Idaho, and Wyoming. About 55% of these swans are year-round residents, breeding at Red Rock Lakes National Wildlife Refuge (RRNWR), Yellowstone National Park (YNP), and on surrounding public and private lands. The remainder migrate north to spend the summer in Canada. The only identified major Canadian breeding area is the 5700 km^2 region lying north and west of Grande Prairie, Alberta, where 219 Trumpeters were censused in 1978 (G. Holton personal communication). Other small breeding populations have been located in southwestern Alberta, the Yukon, Northwest Territories, and the Cypress Hills region of Saskatchewan (B. Turner personal communication).

Historic Status and Distribution

Both in numbers and geographic distribution, the Trumpeter Swans now extant represent only a remnant of the historic population. Distinguishing the Trumpeter from the slightly smaller, native Whistling Swan (*Cygnus columbianus*) is difficult. Consequently, population estimates of Trumpeters prior to their precipitous decline in the 19th century are vague. Banko (1960), in a detailed review of the species' recorded historic occurrence, concluded that the Trumpeter Swan was once abundant and widespread in North America. Its breeding range extended from Alaska across Canada east to Ontario, and south through the plains to Nebraska and northern Missouri. Recent synthesis of additional archaeological, historical, paleontological, and ecological evidence suggests that Trumpeters also bred in the eastern United States as far south as northern Florida. These populations quickly disappeared as settlement advanced westward (Rogers and Hammer 1978).

Although Trumpeters occurred across a vast area of the USA, nesting swans were never abundant throughout the southern limits of their breeding range. They nested mainly in the northern portions of the continent, utilizing primarily the Arctic-Alpine, open and closed

Boreal Forest, and Aspen Parkland Zones. The prairie pothole habitat of southern Canada and the Great Plains marshes were of small importance to the species (Banko 1960, Halladay 1970). South of Alaska, only three significant breeding areas existed in the USA: the Flathead Valley of western Montana, southern Minnesota and northern Iowa, and the presently occupied Tri-state Region (Banko 1960).

Many ornithologists believed that the destruction of the Trumpeter in Canada and the lower 48 states had reduced the species to the verge of extinction by the 1900's (Coale 1915). However, more Trumpeters had survived than was realized at the time, for the existence of the Alaskan population remained unverified until 1954 (Hansen et al. 1971).

Causes of Decline

American Indians and early settlers hunted Trumpeters for food and skins, but it was the commercial swan skin trade and habitat destruction that caused the near extinction of the species outside of Alaska. Between 1772 and 1900, tens of thousands of swan skins were exported by the Hudson Bay Company from the heart of the Trumpeter's Canadian breeding grounds. Human settlement on wintering areas and the more southerly breeding sites reduced important habitat and increased the hunting kill of migrating and wintering swans (Banko

1960). These combined factors reduced the known United States population to less than 100 Trumpeters by 1932. The Canadian population also declined precipitously; by 1916 less than 100 Trumpeters were censused in British Columbia (Morris 1970).

Trumpeter Swans in YNP

The continual occurrence of Trumpeter Swans in YNP seems likely, based on statements or specimens procured by early travelers (Carpenter 1878, Wingate 1886, Hague 1889, Banko 1960, Haines 1965). Skinner sighted up to five Trumpeters in YNP on various occasions between 1915 and 1921. In 1919, Skinner found an active nest on a small pond near Lewis Lake, thus establishing that Trumpeters still bred in the USA. The same year, Smith found six cygnets on a small pond south of Delusion Lake (Skinner 1925).

The Superintendent's monthly report for March 1920 mentioned 20 to 30 Trumpeters wintering on the Lewis and Bechler rivers, indicating winter use of YNP persisted through the population's nadir.

Aside from the protection from shooting that YNP provided the few remaining Trumpeters, no specific management actions to benefit the swans occurred until 1929. At that time, the Wildlife Survey, Department of the Interior, sponsored field observations in YNP conducted by Dr. J. Dixon (Wright 1934).

In 1930, aided by National Park Service (NPS) employees G. Wright and B. Thompson, Dixon attempted to determine the causes of egg loss and juvenile mortality at two nests, in addition to searching the Park for other nests. Four nesting pairs were located.

Wright was specifically assigned to the Trumpeter problem in 1931 and began life history studies. He also conducted the first census of YNP and the Jackson Lake area. From 1931 to 1935, NPS personnel worked vigorously for the protection and preservation of the Trumpeter, both in YNP and in the surrounding areas of Montana, Wyoming, and Idaho. In YNP continued life history studies, the building of a small dam at Swan Lake (Barrows 1936), placement of flags to discourage land crossings (Childs 1934), control of coyotes (Canis latrans) and Ravens (Corvus corax), local closures of fishing to prevent disturbance of nesting swans, construction of two nesting islands, and the relocation of a Park road were all undertaken to aid the Trumpeters (Banko 1960).

Efforts of the NPS culminated in recognition of the Centennial Valley of Montana as important Trumpeter breeding habitat and the establishment of the 16,270 ha RRNWR in 1935 (Banko 1960).

Subsequent studies of Yellowstone Trumpeters by Park personnel (Childs 1934, Wright 1934, Barrows 1936 and 1937, Oberhansley and Barrows 1939, Condon 1941) added much valuable information on the life history, nesting success, and distribution of swans in YNP. In addition to assigning employees to swan research, the NPS became actively involved in a swan interpretive program. Illegal shooting along the Henry's Fork of the Snake River in Idaho caused significant losses of Trumpeters. To combat this loss, the NPS participated in a 2-year cooperative series of lectures which reached 24,687 people and fostered pride and awareness among the local residents (Banko 1960).

Although Wright made the first census in 1931, certain important habitat, particularly the Red Rock Lakes area, was not discovered and included in surveys until 1932. Realizing the inadequacy of ground surveys, Wright recommended that an aerial census be conducted in 1934 (Wright 1934). However, the ground censuses continued annually until 1946 when the area was partially surveyed from aircraft. In 1948, the first complete regional aerial survey, including all of YNP, was flown (YNP files).

The USFWS flew annual late-summer swan censuses through 1968 with the cooperation of the NPS. When the Trumpeter was removed from the rare list of the USFWS Red Book (Trumpeter Swan Society 1969) in 1968, surveys were changed to a tri-annual schedule. Subsequent late-summer aerial censuses took place in 1971, 1974, and 1977.

Although no detailed swan studies were conducted in YNP after Condon's work in 1939 and 1940, intermittent observations by

Park employees and the Tri-state USFWS surveys suggested very low cygnet production since about 1960. Page (1976) studied Trumpeters at RRNWR and assumed that the recent poor reproductive success in YNP was due to human disturbance of nesting swans. This view was repeated in the popular literature (Whitmore 1974) and in the 1974 USFWS swan survey report. The continued increase in Park visitation and backcountry use during the 1960's and 1970's, and the assertion that this activity was adversely impacting the Trumpeters prompted the NPS to support this study.

The primary purpose of the NPS in administering natural areas such as YNP is to maintain the area's ecosystem in as nearly pristine a condition as possible. Research primarily involves documenting pristine conditions and processes, and determining the completeness of the Park ecosystem. Management generally involves the maintenance or restoration of natural ecological relationships (Houston 1971). Guided by this philosophy, low reproductive success among Trumpeters in YNP is not a cause for management concern unless the factors responsible are man-caused. My primary goals in this study were to assess the current breeding status of Trumpeters in YNP, and to determine whether human activities within the Park were contributing to the decline in cygnet production.

Objectives of This Study

Initial study objectives were to:

1) determine the number of nesting pairs, the chronology, rates, and causes of nest failures and cygnet mortality;
2) evaluate the effects of human activity at nesting territories;
3) quantify the constancy of incubation at successful and unsuccessful nests;
4) identify significant characteristics of successful and unsuccessful territories; and
5) provide remedial management recommendations.

As the problems involved in the reproductive failures became apparent, and with the discovery of large numbers of migrant Canadian Trumpeters in YNP, I expanded the study. The swans were followed from October to December 1976, October to April 1977-78, and October to April 1978-79.

Added objectives were to:

6) locate and individually identify all neck-banded Trumpeters that migrate into YNP;
7) determine the species, number, and patterns of habitat use of migrant swans in YNP; and
8) follow the winter movements of neck-banded Trumpeters throughout the Tri-state Region and identify sites of concentrated winter use.

Objective number 4 was abandoned because the Trumpeters normally remained on their territories throughout the ice-free period. Sampling habitat parameters such as water chemistry, submerged vegetation, invertebrates, etc., would have caused some swans to abandon their territories.

CHAPTER II

STUDY AREA DESCRIPTION

Location

The study area encompassed 6400 km^2 of northwestern Wyoming and contiguous portions of Idaho and Montana (Fig. 1). While nesting studies concentrated on swans in YNP with peripheral observations in the Targhee and Gallatin National Forests, migration studies followed the swans throughout this Tri-state Region. The Henry's Fork of the Snake River in the vicinity of Harriman State Park, Idaho, was the focus of winter observations.

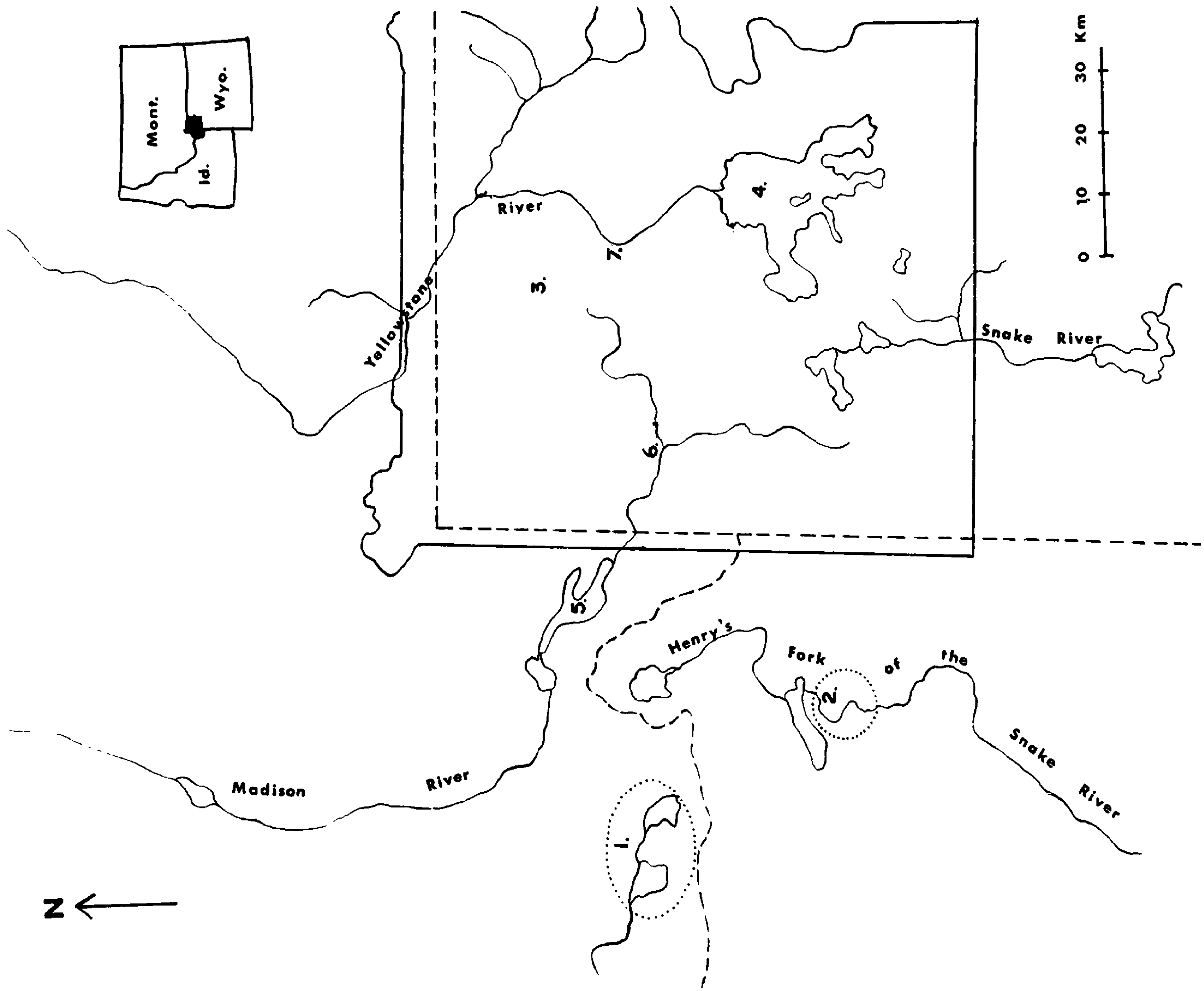
Administration

Management of the Trumpeter Swan and its habitat within the study area is a responsibility of the following agencies: the U.S. Fish and Wildlife Service, U.S. National Park Service, U.S. Forest Service, Bureau of Reclamation, the Fish and Game Departments of Idaho, Montana and Wyoming, and the Idaho Department of Parks and Recreation. From April through October, the migrant portion of the population resides in Canada where it is subject to Federal and Provincial jurisdictions. The variety of agencies and their differing

Fig. 1. Map of Yellowstone National Park and vicinity study area.

Legend

1. Red Rock Lakes National Wildlife Refuge
2. Harriman State Park
3. Yellowstone National Park
4. Yellowstone Lake
5. Hebgen Lake
6. Madison Junction
7. Canyon Village



Mont.
Wyo.
Id.
Yellowstone
River
Snake River
Henry's Fork of the Snake River
Madison River
Km
0
10
20
30
1.
2.
3.
4.
5.
6.
7.
N

management philosophies greatly complicates coordinated management of the midcontinental Trumpeter population.

Physiography

The greater part of YNP is a forested plateau, cut by headwaters of the Yellowstone, Madison, Gallatin, and Snake rivers, and traversed from west to southeast by the Continental Divide. Much of the Park lies between 2128 and 2432 m in elevation. The northern portion, the southwestern corner, and the areas outside the Park generally are between 1824 and 2128 m in elevation. Mountain ranges encircle the plateau except to the southwest.

Over 300 lakes dot the region, ranging from less than 1 to over 35,990 ha in size. Geysers and hot springs provide surface evidence of the region's volcanic history, and runoff from thermal features allows a few stretches of the major rivers to remain ice-free during the coldest weather.

Keefer (1972) provides further details of area geology.

Weather

Short cool summers and long cold winters characterize the area. Snow accumulation begins by early November and snow lingers at the higher-elevation nesting territories in YNP until June. Average snowfall varies from 230 to 500 cm at weather stations throughout the area.

Winter daytime temperatures of -10 to -5°C are common at the wintering sites but occasional cold spells with temperatures below -40°C occur almost every year. Although spring warming begins by March, snow has fallen during every month of the year in YNP. Severe May and June storms regularly bring snow or hail.

The varied topography of the area results in great weather variation from one location to another, particularly on opposite sides of the Continental Divide. More than one major weather system may affect different portions of the study area on any given day.

Average annual precipitation at weather stations in YNP varies from 37.16 cm at Mammoth to 83.84 cm at Snake River Ranger Station, with the greatest monthly precipitation falling in June. Mean annual precipitation in excess of 203 cm occurs near Heart Lake in YNP (Farnes 1973). Mean annual temperature varies from 4.3°C at Mammoth to .22°C at Yellowstone Lake and the average frost-free period lasts 91 days, from 8 June to 7 September (Martner 1977).

Weather during the years of the study varied considerably (Table 1). The 1977 nesting season was relatively mild and dry, and snowpack during the preceding winter was less than 50% of normal (YNP files). The greatly reduced runoff minimized spring flooding and left many lakes and ponds, including Yellowstone Lake, with near record low water levels by June.

Table 1. Temperature and precipitation during incubation and brood rearing.

	Temperature (°C)					Precipitation (cm)				
								No. of days		
	Av. max.	Av. min.	Av. temp.	Departure from normal	No. days min. below 0°C	Total	Departure from normal	> .25 cm	> 1.27 cm	> 2.54 cm
1977										
April	14.3	-7.4	3.4	1.6	M	0.6	-2.8	1	0	0
May	15.1	-1.78	6.7	-0.3	27	5.9	0.6	8	0	0
June	23.8	1.6	12.7	2.1	11	4.2	-2.4	7	0	0
July	26.7	2.2	14.4	-0.3	7	6.2	2.5	6	1	0
1978										
April	9.6	-4.7	2.4	0.6	M	2.5	-0.9	4	0	0
May	13.6	-2.4	5.6	-1.4	26	5.3	0.0	5	1	0
June	20.8	-0.2	10.3	-0.3	19	2.7	-3.9	4	1	0
July	24.3	2.3	13.3	-1.4	5	2.6	-1.0	4	0	0

M = missing data.

In 1978, the weather was cool with close to normal precipitation in April and May. March snowpack in YNP was 142% of normal (YNP files). Runoff peaked in late May and early June, causing a sudden rise in water level from the very low levels of the previous winter. Yellowstone Lake rose to near its highest recorded level.

CHAPTER III

METHODS

Aerial Surveys

Nest locations, nesting chronology, brood size, and cygnet survival were recorded during aerial surveys using a Piper Super Cub.

Nine surveys were flown in 1977 at approximately 2-week intervals beginning on 7 April and ending on 30 July. A final flight on 25 September provided a census of the entire study area. Eight flights, beginning on 9 May and ending on 12 August, provided information on the 1978 nesting effort. On a final flight on 16 September I recorded cygnet production.

Flights in April and May covered the entire study area and required about 4 hours flight time to view all potential nesting sites. Subsequent flights included only the active nesting territories and required progressively less time ($2\frac{1}{2}$ hours or less) as nests failed and were deleted from the survey.

Ground Observations

Ten nesting territories could be reached within an hour's hike from a road. I visited each of these areas two or three times per week during the incubation and brooding periods. The behavior of each pair of swans in response to humans was observed and the existing levels of human activity were recorded. Evidence relating to nesting failures and cygnet mortality was retrieved. I usually viewed the swans from a concealed position using a Questar Field Telescope unless the nesting attempt had failed. In that case, I examined the nest and collected egg shell fragments, unhatched eggs, and dead cygnets.

Access to the other 21 territories involved either an initial 240 km drive (to nests in the Targhee National Forest), a full day's hike, or both. Each of these nests was visited as soon after the expected hatching date as possible, or as soon as aerial observations revealed a nesting failure.

Time-lapse Photography

Time-lapse photography was used to record the incubation pattern at selected nests. My primary purpose was to determine the constancy of incubation, i.e., the proportion of the daylight hours that a swan actually spent incubating, and the frequency and duration of recesses, or absences from incubation (Skutch 1962).

Minolta Autopak-8 cameras, enclosed in modified metal ammunition boxes for protection, were mounted on a tree trunk, usually at least 100 m from the nest. With exposures at either 2- or

3-minute intervals, each role of film lasted 7 to 10 days. A photo-electric cell shut each camera off during the night.

Migration Studies, Yellowstone Lake Area

My census route began at Canyon Village and followed the road along the Yellowstone River to Yellowstone Lake. At Fishing Bridge Junction, it ran east along the lakeshore to Mary Bay, then returned to the Junction and followed the lakeshore south to Gull Point Drive where the census ended (Fig. 8). The excellent road access and the fortuitous location of good observation points greatly facilitated the censusing. All areas of water not visible from the road were visited on foot. Every time a group of swans was encountered, I recorded the:

1) species of each bird;
2) age (adult or cygnet) of each bird;
3) size of broods;
4) color and code number of neck-bands;
5) presence of tarsal-bands;
6) injuries, deformities, or abnormal coloration; and
7) site location.

Species Identification

Because Whistling Swans and Trumpeters joined in mixed flocks during autumn and winter, I took great care to distinguish the species of each swan. The characteristics used in field identification, in order of their usefulness, were:

1) Vocalizations. Warning notes and flight calls of each species are quite distinctive. The common names of the two species are fairly descriptive of their respective tonal qualities. When identification of a particular bird was in doubt, I slowly revealed my presence, causing the bird to utter an alarm call which revealed its identity. Usually the migratory and wintering groups of 5 to 100 swans were quite vocal, thus facilitating identification.

2) Lores. All but three Whistlers observed during the study possessed yellow pigment on the lores. This character was absent from all but one Trumpeter which possessed abnormally pigmented legs as well.

3) Size. In groups composed of both species, the smaller size of the Whistling Swan (average 6.3 to 7.3 kg) contrasted noticeably with that of the Trumpeter (average 10.3 to 12.7 kg) (Bellrose 1976).

4) Culmen profile. As noted by Delacour (1954) and Hansen et al. (1971), the Whistling Swan possesses a concave culmen, while that of the Trumpeter appears nearly straight, giving the bill a heavier, wedge-shaped appearance.

5) Cygnet coloration. From October through March, the plumage of Whistling Swan cygnets was noticeably paler than that of the Trumpeter cygnets. This difference became progressively more

apparent. By March, when Trumpeter cygnets were still a rather uniform medium gray, Whistling Swan cygnets were very pale gray with a darker head and neck. Cygnets of both species possess a flesh-colored bill with a gray distal tip and gray nail. On Trumpeter cygnets, however, the base of the bill is also gray, much darker than that of the average Whistler.

Although overlap in several of these criteria occurs between the species, their collective use made identification possible under all but the most difficult viewing conditions.

Censuses in Idaho

Swan observations at Harriman State Park were difficult because of the lack of concealing cover which could permit close approach to the birds, and snow depths exceeding 1.5 m. I used a snowmobile to reach observation points usually 500 or more meters from the swans. Data were gathered only when light conditions permitted the use of the Questar telescope. Due to the difficulty of approach, I usually recorded only ages, neck-band codes, and the total number of swans present. Occasionally, with optimal light conditions, I identified the less numerous Whistlers.

Sampling of Aquatic Vegetation

Feeding areas in YNP and Harriman State Park were examined to determine the species composition and relative abundance of the aquatic vegetation. The work was accomplished in October 1977 prior to the arrival of migrant swans.

Wearing a wet suit I first walked through the feeding sites, observing the location of feeding pits and obtaining an overview of the vegetation present. Transects perpendicular to the current were then marked with stakes on each bank and the vegetation composition was sampled at regular intervals along the transect. Usually six samples were taken per transect.

Sampling was accomplished using a forceps-like device borrowed from RRNWR. The device cut off and held vegetation from approximately a 0.092 m^2 (1 ft^2) area of river bottom. Samples were wrung by hand to remove excess water, sorted by species, and weighed to obtain the relative percent occurrence of each species.

Locations greater than 2 m in depth were not sampled. Most plants in such areas lay beyond the reach of feeding swans.

Territory Names

Names of territories follow the nomenclature appearing on USGS topographical maps of the study area. Where no official name existed, I followed local usage or chose a geographically descriptive name. These unofficial names appear in quotations throughout the text. Precise territory locations were described using Universal Transverse Mercator (UTM) coordinates for management use. This information is retained by the Biologist's Office, YNP.

CHAPTER IV

RESULTS

Spring and Summer Observations

Spring thaw. Nesting territories at elevations less than 2011 m were ice-free by 26 April 1977 and 18 April 1978. On the higher plateaus, between 2094 and 2530 m elevations, the nesting lakes remained frozen until at least 30 April 1977 and 21 May 1978. The last territories to thaw, Riddle, Grebe, and Cygnet lakes, remained substantially frozen into the first week of June 1978. Small areas of open water occurred at lake inlets, outlets, and around lake perimeters near submerged springs 3 or more weeks before the main portion of the lakes became free of ice.

Arrival at territories. Depending on elevation and rate of thaw of the site, Trumpeters arrived at their territories between late March and the middle of May, appearing 2 or 3 weeks before nesting sites were available or lakes were ice-free. The swans loafed on the ice, drove off other Trumpeters, and made excursions, presumably to forage on nearby bodies of open water. Swans often used the extremely limited open waters within their territories, pushing through the rotting ice to reach submerged aquatic vegetation.

The pair that nested at "Madison River #1" in 1978, remained through the preceding winter on the ice-free River within 3 km of their 1977 nest. They began to display territorial behavior near the nesting site in March when they drove off their three 10-month old cygnets and at least two adults.

The nesting pair at Harlequin Lake in 1977 arrived unusually late. Although the Lake was ice-free by 30 April, the swans remained 1 km distant on the Madison River and did not occupy the territory until 31 May.

Location and status of territories. Trumpeters occupied 31 territories, and attempted to nest in all but one (Grebe Lake). Territory location and status are summarized in Tables 2, 3, and 4. The term "occupied" refers to all territories where swans were present and displayed territorial behavior, regardless of whether or not nesting occurred. The presence of both a pair of swans and a freshly built nest characterized "active" territories. This category included actual nesting attempts as well as other unclear situations where nest building occurred, but egg laying was not verified. Five territories were unoccupied during one of the two summers.

Characteristics of territories. Four territories were on rivers in areas where numerous islands and extensive braided channels existed. The remaining 27 territories were on widely

Table 2. Status of territories, 1977 and 1978.

Name	Status 1977	Status 1978	Area
1. "Geode Pond"	N*	X	YNP
2. "Delta South"	N*	N	YNP
3. Riddle Lake	N*	N*	YNP
4. "Madison River #1"	N*	N	YNP
5. "Trumpeter Lake"	N	N	YNP
6. East Tern Lake	N	N	YNP
7. White Lake	N	N	YNP
8. Cygnet Lake	N	N	YNP
9. "Delusion Pond South"	N	N	YNP
10. "Trail Creek Pond"	N	N	YNP
11. "Calf Creek Pond"	N	N	YNP
12. "Little Robinson Pond"	N	N	YNP
13. Harlequin Lake	N	O	YNP
14. "Bunsen Peak Pond"	N	X	YNP
15. "Delusion Pond North"	P	P	YNP
16. "Richards Creek Pond"	P	P	YNP
17. Swan Lake	O	N	YNP
18. "Foster Lake"	O	N@	YNP
19. "Beach Spring Lagoon"	O	N	YNP
20. Grebe Lake	O	O	YNP
21. "Madison River #2"	X	N*	YNP
22. "Delta North"	X	N	YNP
23. Aldridge Lake	N*	N	GNF
24. Thompson Hole	N*	N*	TNF
25. Widgit Lake	N*	N	TNF
26. Rock Lake	N	N	TNF
27. Indian Lake	N	N	TNF
28. Winegar Hole	X	P	TNF
29. Chain Lake	?	N*	TNF
30. Ernest Lake	?	N	TNF
31. "Long Meadow Pond"	?	N	TNF

N* = active nest, cygnets fledged
N = active nest, no cygnets fledged
P = active nest, incubation uncertain
N@ = nest shared by two females
O = occupied, no nest
X = swans not regularly present
? = area not surveyed in 1977

Table 3. Summary of territories, 1977 and 1978.

	Active nests				
	Documented incubation	Questionable incubation	Occupied no nest	Vacant	Not surveyed
1977	19	2	4	3	3
1978	24	3	2	2	0
Total	43	5	6	5	3

Table 4. Location of occupied territories, 1977 and 1978.

	Yellowstone National Park	Gallatin National Forest	Targhee National Forest	Total
1977	20 (16)*	1 (1)	4 (4)	25 (21)
1978	20 (18)	1 (1)	8 (8)	29 (27)
Total distinct territories	22 (21)	1 (1)	8 (8)	31 (30)

*Number of active territories in parentheses.

scattered lakes. With the exception of the two Madison River territories which overlapped spatially, though not temporally, all territories were at least 2 km apart. Most nesting lakes were separated by more than 10 km of forest.

Nesting lakes ranged from 1.2 to 110.8 ha in size, and from 1770 to 2515 m in elevation. Territory size was dictated by the size of the lake; median size was 10.7 ha.

Although volcanic rhyolite flows cover substantial portions of the study area (Keefer 1972), all territories occurred on basalt or Quatenary detrital deposits (USGS 1972). Lakes on the rhyolite flows are typically dilute, slightly acid, and of low productivity (J. Varley personal communication).

<u>Use of territories</u>. At least four nonterritorial pairs moved from lake to lake, particularly in the northern portion of YNP. Other nonbreeding Trumpeters summered in the Targhee National Forest (TNF) but were not systematically censused. Because Trumpeters do not nest until at least their third, and more frequently their fourth or fifth year (Scott 1972), it is likely that these birds were reproductively immature.

That some competition for territories exists was evident in 1978 when a nonbreeding pair of swans moved into the periphery of the active "Madison River #1" territory. The occupants were incubating normally when, on 15 May, flood waters destroyed the nest. By 29 May, the intruders took over the territory and nested successfully, eventually fledging one cygnet. The original residents remained near their destroyed nest throughout the summer, about 500 m downstream from the new active nest. The numerous islands at this site provided visual barriers which may have lessened territorial interactions between the two pairs. On 29 April 1979, two pairs returned to the territory and engaged in a fierce struggle. Human intervention prevented the victor from drowning its badly weakened opponent (J. Foote personal communication).

YNP encompasses over 200 lakes greater than 0.4 ha in size (Condon 1941). Many are unsuitable for nesting because of high elevation, oligotrophic conditions, fluctuating water levels, or unusual water chemistry. Thirty-seven lakes have been used by nesting Trumpeters at least once between 1931 and 1978 (Appendix A). Only 11 lakes have successfully fledged broods during 5 or more years, contributing some 78% of all cygnets fledged in YNP.

Of these 11 historically most productive territories, seven contained nests during this study, but only one (Riddle Lake) fledged young. The four lakes where nesting no longer occurs have fledged no cygnets for from 13 (Robinson Lake) to 26 years (Grebe Lake). Two of these territories, Shoshone and Grebe lakes, sustained heavy day use as well as overnight use in excess of 7500 and 880 visitor-nights, respectively (YNP files). The almost constant presence of campers and fishermen rendered the limited shoreline nesting habitat unusable. Swans intermittently visited Shoshone Lake and displayed territorial behavior at Grebe Lake, but they made no attempt to nest at either location. Robinson Lake may no longer be suitable due to eutrophication; much of its area now dries out during the summer. Swans investigated Geode Lake in April 1977 but left it to nest on a nearby small pond ("Geode Pond") which offered more abundant aquatic vegetation. The presence of an active Canada Goose (Branta canadensis) nest at Geode Lake may have contributed to the swan's departure.

Three territories had no prior record of use, but they all are quite inconspicuous small ponds ("Trail Creek Pond," "Calf Creek Pond," and "Richard's Creek Pond") that could easily have escaped notice in past surveys.

Territorial behavior. Nesting pairs were highly territorial, seldom tolerating the presence of other swans on the nesting lake or in the air overhead. In seven observed conflicts, the defending male met intruders with a running charge which put them to flight, then returned to his mate at the nest and a mutual triumph display (Banko 1960) followed. Although display and chases were the most common means of territorial defense, as previously mentioned a battle at the

Madison River territory could well have proven fatal to the loser. This extreme degree of territorial defense most likely evolved out of the unusual nesting events in that territory in 1978.

Trumpeters also occasionally chased Canada Geese but this species nested primarily along the rivers and conflict was minor. In two instances (Riddle Lake and "Madison River #1"), the breeding adults permitted another swan to enter the territory after the third week of incubation. In both cases, the intruder was possibly the pair's yearling offspring.

Despite their normally strong territoriality, nesting Trumpeters occasionally left their nests completely unguarded during the incubation period. At both Aldridge and Trumpeter Lakes, the pairs habitually flew off together to feed at other ponds up to 2.5 km distant. Absences from the nesting lake of up to 70 minutes were observed.

Nest initiation. Nest building did not commence until the chosen site was snow-free. At sites below 2011 m elevation, a 3- to 4-week interval between arrival and nest initiation was common. In contrast, at Cygnet and Riddle lakes, the last to thaw, nest initiation followed within a few days of arrival.

In 1977, all nest building began between 30 April and 30 May; successful nests were initiated between 5 and 14 May. Although the

1978 nest initiation period was virtually identical, 29 April to 29 May, successful nests were initiated between 15 and 29 May. Despite the similarity in the range of dates between years, initiation was delayed 1 to 3 weeks at certain territories in 1978.

Nest location and construction. Of 44 nests examined, 10 were built on abandoned beaver (*Castor canadensis*) lodges, 24 were piles of vegetation heaped by the swans onto islands, and 10 were offshore mounds of aquatic vegetation piled up until they rose above the water surface. Use of muskrat (*Ondatra zibethica*) houses was not detected although a few nests might have buried a muskrat house. No significant differences in nesting success ($p = 0.05$, $X^2 = 0.765$, d.f. = 1) or cygnet survival ($p = 0.05$, $X^2 = 4.09$, d.f. = 1) existed among nest types.

If a territory contained an island, the island was always the chosen nesting site. Island size ranged from less than 1 m^2 to about 2.6 ha. Swans scraped the available terrestrial vegetation (mainly sedges and grasses) into a pile that they shaped with their bills. This type of nest rarely exceeded 1.5 m in diameter. On White Island, where vegetation in the vicinity of the nest was lacking, the swans incubated on a dense mound of humus. This nest lacked any recognizable vegetation in its composition.

Swans that nested on beaver lodges merely flattened an area on top of the lodge and built the nest out of lodge materials. When the lodge contained large chunks of peat and a high proportion of mud, those materials were scraped together to form a soft nest. The "Delusion Pond South" nest, however, sat on a very weathered beaver lodge and was made solely of sticks, ranging up to 1 m in length. Beaver lodges were usually without dry vegetation with which to cover the eggs during the female's absences, but provided the maximum available relief, and thus protection, from rising water levels.

Fate of nesting attempts. "Successful" nests were those in which one or more eggs hatched. Nesting success was 71% in 1977 and 41% in 1978. Increased flooding, infertile clutches, and failure to lay eggs caused the significantly lower ($p = 0.05$, $X^2 = 4.47$, d.f. $= 1$) 1978 performance (Table 5).

Several nests failed in the same manner both years. The East Tern Lake nest was made of Myriophyllum exalbescens piled in a mound at the center of the lake inlet. Both years, the spongy nesting material became saturated with water and the swans deserted during incubation. In 1978, they deserted on 1 June, the same day that the fifth egg was laid.

Both the White Lake and "Delusion Pond South" nests were also poorly constructed although adequate materials occurred in each territory. In each case, no suitable materials were used to cover the

Table 5. Fate of nesting attempts.

	Successful hatch	Failures						
		Flooded	Predator	Deserted during incubation	Incubation full term no hatch	Infertile clutch	No eggs	Fate unknown
1977 n = 21	15 (71%)	1 (5%)	0	2 (10%)	1 (5%)	0	2 (10%)	0
1978 n = 27	11 (41%)	4 (15%)	1 (4%)	2 (7%)	2 (7%)	3 (11%)	3 (11%)	1 (4%)
Total n = 48	26 (54%)	5 (10%)	1 (2%)	4 (8%)	3 (6%)	3 (6%)	5 (10%)	1 (2%)

eggs during the female's absences. Swans nesting for the first time probably construct inferior nests, but the repetition of the performance in the second year was puzzling.

Although swans appeared to incubate at "Richard's Creek Pond" and "Delusion Pond North," searches produced no evidence of eggs when the birds left the nests. Both pairs repeated this performance in 1978, and I suspect they either suffered from a physiological abnormality that interfered with egg laying or were not reproductively mature.

Four nests were flooded in 1978, when the peak runoff came in late May and early June. Water level in most small ponds rose 20 to 40 cm above early May levels and the Yellowstone and Madison rivers flowed over their banks. All three river nests ("Madison River #1," "Delta North," and "Delta South") were flooded as well as the nests at East Tern Lake and "Delusion Pond South." The "Delta North" nest was not counted as a flood loss because it failed prior to the flood.

One nesting effort was destroyed by predation. On 21 May 1978, the "Delta North" pair was found nesting in willows in the braided delta of the Yellowstone River, amidst a 9 km^2 area of marsh and stream channels. When next observed on 1 June only one adult was present and the scattered remains of the second lay on the nest. The lone adult remained near the nesting site throughout the summer.

Clutch size. Clutch size was determined at 33 nests (Table 6). The risk of disturbance at the other 15 nests was too great to justify close contact. The reduction in clutch size in 1978 was highly significant ($p = 0.025$, $t = 2.29$, d.f. $= 31$).

Table 6. Means and frequency distribution of clutch sizes.

		Number of eggs in clutch						
	Mean	1	2	3	4	5	6	7
1977 (n = 13)	4.85	0	0	1	3	6	3	0
1978 (n = 20)	3.80	1	4	3	4	6	2	0
Total (n = 33)	4.21	1	4	4	7	12	5	0

Fate of eggs. Table 7 summarizes the fate of eggs from 32 clutches of known size; hatching success in this group was 62%. In addition, 5 nests probably lacked eggs, 1 possessed two clutches of infertile eggs, and 10 had clutches of undetermined size. In 1977 and 1978 combined, those 10 nests hatched 12 cygnets from an estimated 44 eggs for a hatching success of 27%. Hatching rate was low in this group for the same reason that clutch size could not be determined, i.e., several nests failed completely during incubation and the eggs disappeared.

Table 7. Fate of eggs at 32 nests.

	No. eggs laid	No. hatched	Unhatched eggs: No. infertile	No. partly developed	No. fully developed	Condition unknown	Flooded*
1977 13 nests	63	45 (71%)	8 (13%)	6 (10%)	4 (6%)	0	5# (8%)
1978 19 nests	66	35 (53%)	6 (9%)	4 (6%)	3 (5%)	18 (27%)	14@ (21%)
Total 32 nests	129	80 (62%)	14 (11%)	10 (8%)	7 (5%)	18 (14%)	19 (15%)

*Eggs damaged by flooding, condition of those retrieved given under "unhatched."

#East Tern Lake., nest flooded; two infertile, three partly developed eggs.

@"Madison River #1," East Tern Lake, and "Delta South" nests flooded; condition of eggs unknown.

Using the known mean clutch sizes for each year, I estimated egg production and hatching rates for the 42 nests that contained normal clutches (Table 8). Hatching success in 1978 was significantly lower ($p = 0.05$, $X^2 = 4.77$, d.f. = 1) than in 1977. However, when eggs lost to flooding were disregarded, the hatching success of the remaining eggs did not differ significantly ($p = 0.05$, $X^2 = 1.44$, d.f. = 1) between years.

Table 8. Estimated egg production and percent hatching, all clutches.*

	No. of clutches	No. of eggs	No. hatched (%)
1977	19	92	52 (57)
1978	23	87	35 (40)
Total	42	179	87 (49)

*Six nests containing abnormal clutches not included.

Egg measurements. The mean width and length of 45 eggs was 73.75 mm (SD = 2.05) and 114.19 mm (SD = 3.66) (Appendix B). This is smaller than Alaskan eggs which averaged 75.0 mm by 117.4 mm (Hansen et al. 1971) and slightly larger than previous mean measurements of eggs from RRNWR of 72.4 mm by 110.9 mm (Banko 1960).

Pesticide analysis. One dead egg from each of six nests ("Delusion Pond South," "Madison River #1," "Bunsen Peak Pond," East Tern, Cygnet, and Riddle lakes) was sent to Patuxent Wildlife

Research Center for organochlorine analysis in 1977. Eggs were analyzed for p,p'-DDE, p,p'-DDD, p,p'-DDT, Dieldrin, heptachlor epoxide, oxychlordane, cis-chlordane, trans-chlordane, cis-nonachlor, Endrin, Toxaphene, PCB's, HCB, and Mirex. The sensitivity of detection limit for all analyses was such that the presence of 0.05 ppm of p,p'-DDE in the eggs would have been recognized. Within these limits all the eggs were clean except for 0.36 ppm p,p'-DDE wet weight in the egg from Riddle Lake. Eggshell thickness of five eggs was between 0.77 and 0.79 mm. Shell thickness of the Riddle Lake egg was 0.65 mm. Patuxent concluded that the egg deaths were not accompanied by significant organochlorine contaminations (S. Haseltine personal communication).

Abnormal nesting. Two adjoining nests, each containing a clutch of five eggs, were maintained by the breeding pair at Foster Lake in 1978. Both swans incubated for at least 60 days at which time the eggs were collected and found to be infertile. Apparently both swans were females and no male was involved in the nesting attempt. Similar situations have occurred at Malheur NWR, Oregon (Scharff 1971), and at La Creek NWR, South Dakota (D. Hammer personal communication.

Incubation. Incubation patterns were quantified at six nests in 1977. Terminology used to describe the events borrows from

Skutch (1962). Constancy is the percent of daylight hours spent on the nest by the incubating bird. Activities were divided between recesses (time off the nest) and sessions (time on the nest). Recesses were further classified as to whether or not the swan covered her clutch with vegetation prior to departing. The summarized data appear in Table 9.

When undisturbed, the incubating female always covered her eggs with dry vegetation from the nest before departing. This procedure usually took from 3 to 5 minutes, during which the bird stood above the eggs and pulled vegetation over them as she slowly turned in a circle. Occasional bouts of preening and stretching interrupted the effort. When disturbed by humans during incubation, most swans slipped into the water and departed without covering the eggs. Twice I observed an incubating bird slip off the nest to aid her mate in territorial defense, then return and cover the eggs before continuing the recess.

Incubating swans usually took three to five recesses per day, each averaging 37 minutes in length (Figs. 2 and 3). The few days when no recesses were taken were invariably cold and snowy. Approximately 67% of all recesses were between 10 and 40 minutes in length, but additional field observations showed that recesses may last at least 314 minutes, as noted at Trumpeter Lake during the second week of incubation.

Table 9. Summary of incubation data.

	Madison R. #1	L. Geode Pond	Aldridge Lake	Harlequin Lake	Cygnet Lake	Bunsen Pk. Pond	All nests
Clutch size	6	5	6	4	4	4	4.8
No. hatched	3	5	6	4	2	1	3.5
No. fledged	3	2	2	0	0	0	1.2
Constancy	89%	88%	86%	78%	88%	81%	85%
daily range	80-96%	78-100%	58-97%	59-94%	75-96%	71-95%	58-100%
No. Recesses/Day	n=20	n=21	n=10	n=16	n=9	n=27	n=103
mean	3.4	3.7	2.5	4.8	4.1	4.4	3.9
mode	4.0	5.0	3.0	4.5	4.0	4.5	4.0
range	1-5	0-6	1-5	2-8	3-6	2-7	0-8
Recess Length (eggs covered)	n=64	n=84	n=19	n=72	n=36	n=109	n=384
mean	32 m	31 m	42 m	48 m	31 m	37 m	37 m
mode	30 m	15 m	35 m	45 m	25 m	35 m	30 m
range	5-58 m	6-54 m	7-111 m	4-126 m	9-70 m	10-96 m	4-126 m
Recess Length (eggs uncovered)	n=4	n=3	n=6	n=0	n=10	n=15	n=38
mean	19 m	11 m	73.2 m	...	21 m	36 m	34 m
mode	...	12 m	45 m	...	25 m	35 m	25 m
range	5-38 m	9-12 m	15-138 m	...	9-42 m	12-60 m	5-138 m
Session Length*	n=52	n=65	n=16	n=56	n=33	n=91	n=316
mean	222 m	108 m	126 m	82 m	143 m	132 m	133 m
mode	90 m	90 m	30 m	90 m	90 m	90 m	90 m
range	8-636 m	27-264 m	3-414 m	4-266 m	3-450 m	4-356 m	3-636 m

*Overnight sessions excluded.

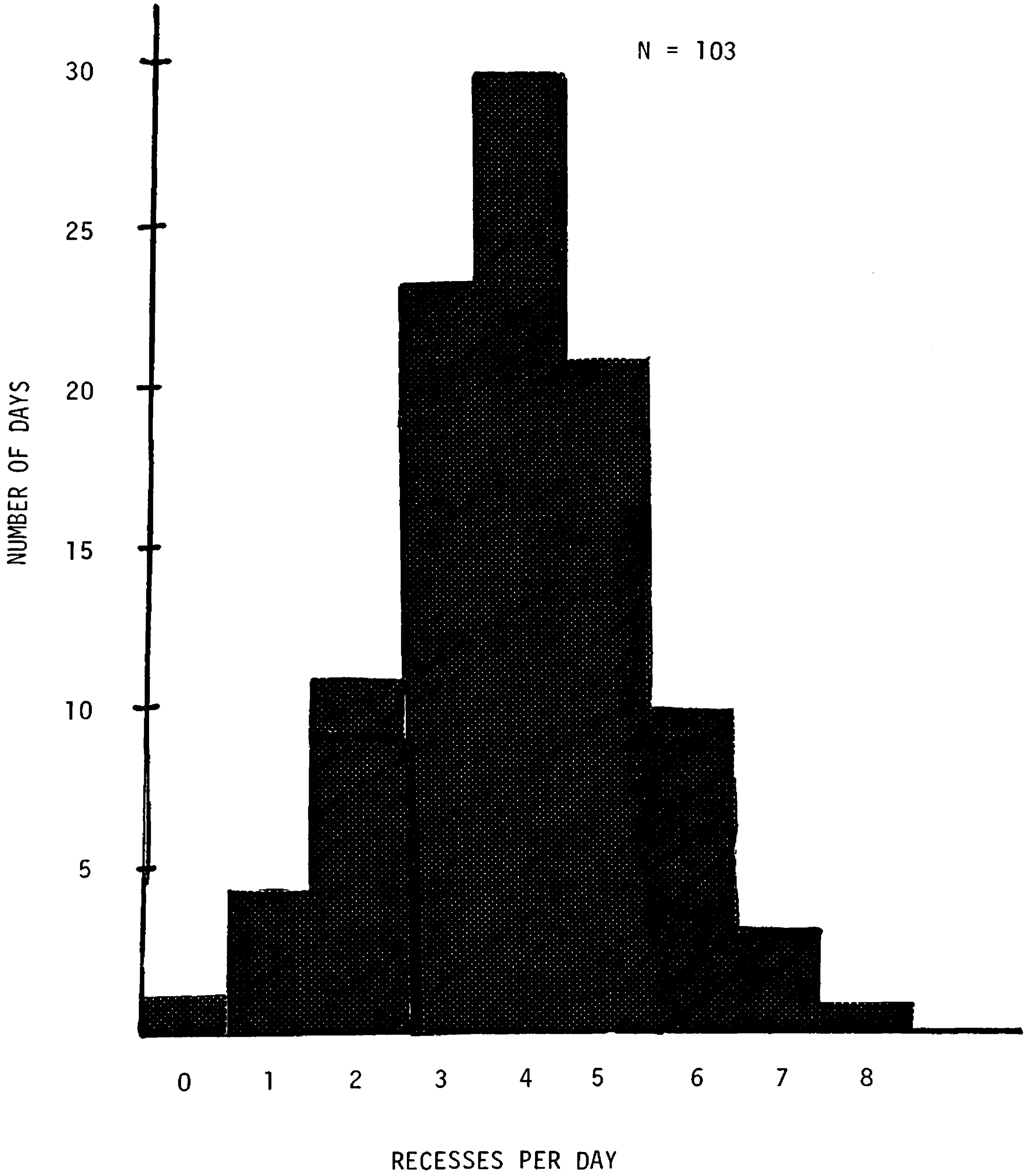


Fig. 2. Frequency distribution of number of recesses/day.

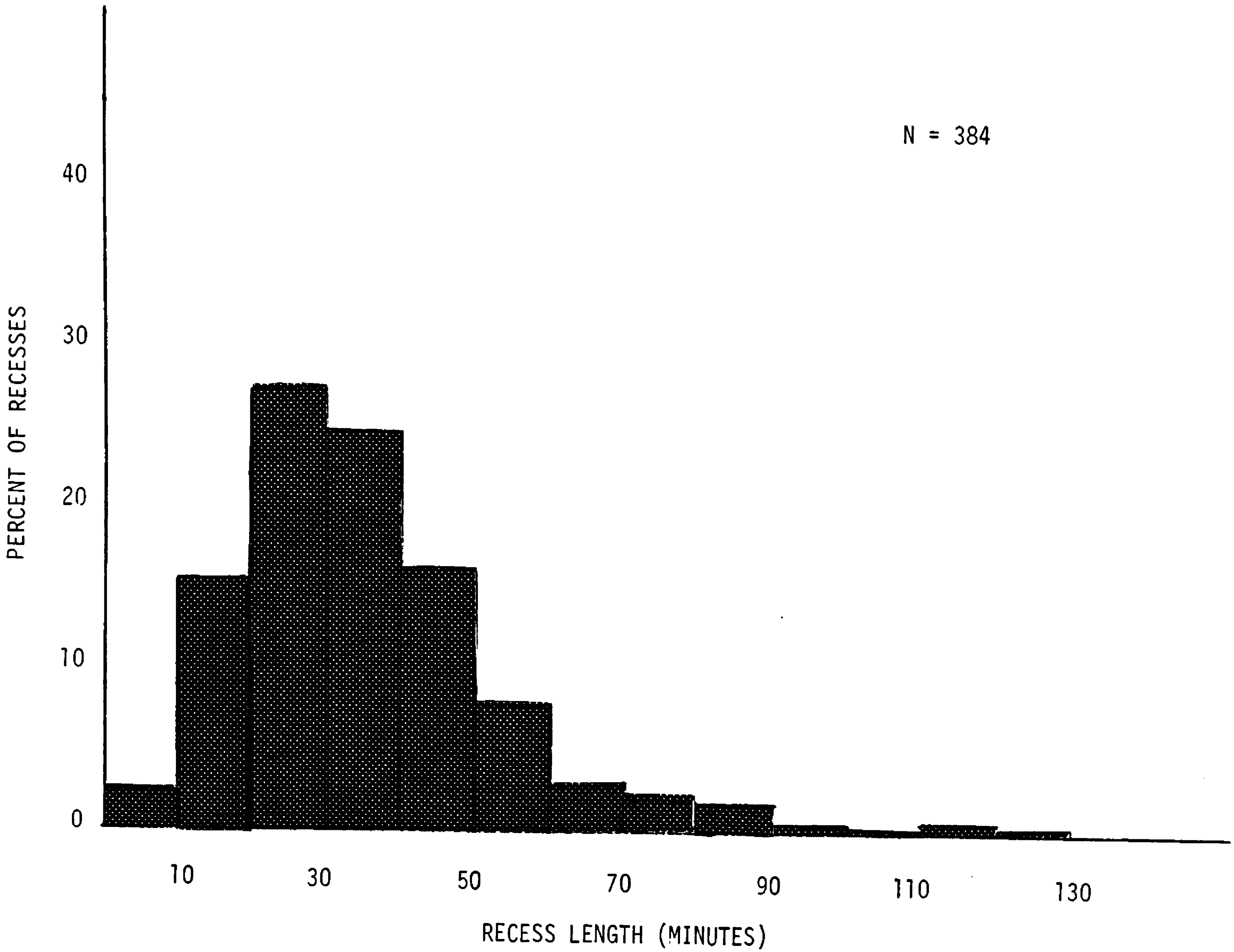


Fig. 3. Frequency distribution of recess lengths.

Overnight session length was not measured, however incubating Trumpeters normally remain on the nest through the night (Cooper 1978). Daylight sessions (n = 316) showed a mean of 133 minutes and mode of 90 minutes (Fig. 4). The frequency distribution of all session lengths was actually bimodal, with overnight sessions lasting at least 15 hours.

Although behavior was quantified at only six nests, the limited data suggest the positive association of several characteristics when the nests are grouped according to their success or failure in fledging cygnets. Nests that fledged cygnets tended to have greater clutch size, hatching success, and constancy, and fewer recesses per day. Multiple regression analysis showed that 89.17% of the variability (r^2) in the number of cygnets hatched could be explained by variation in the number of recesses per day, and session lengths. These same two variables explained 68.54% (r^2) of the variation in number of cygnets fledging.

The data show that the swans which fledged cygnets laid more eggs and were more attentive incubators than those which failed to fledge young. The larger clutch size and increased care were followed not only by increased hatching success but also by increased cygnet viability.

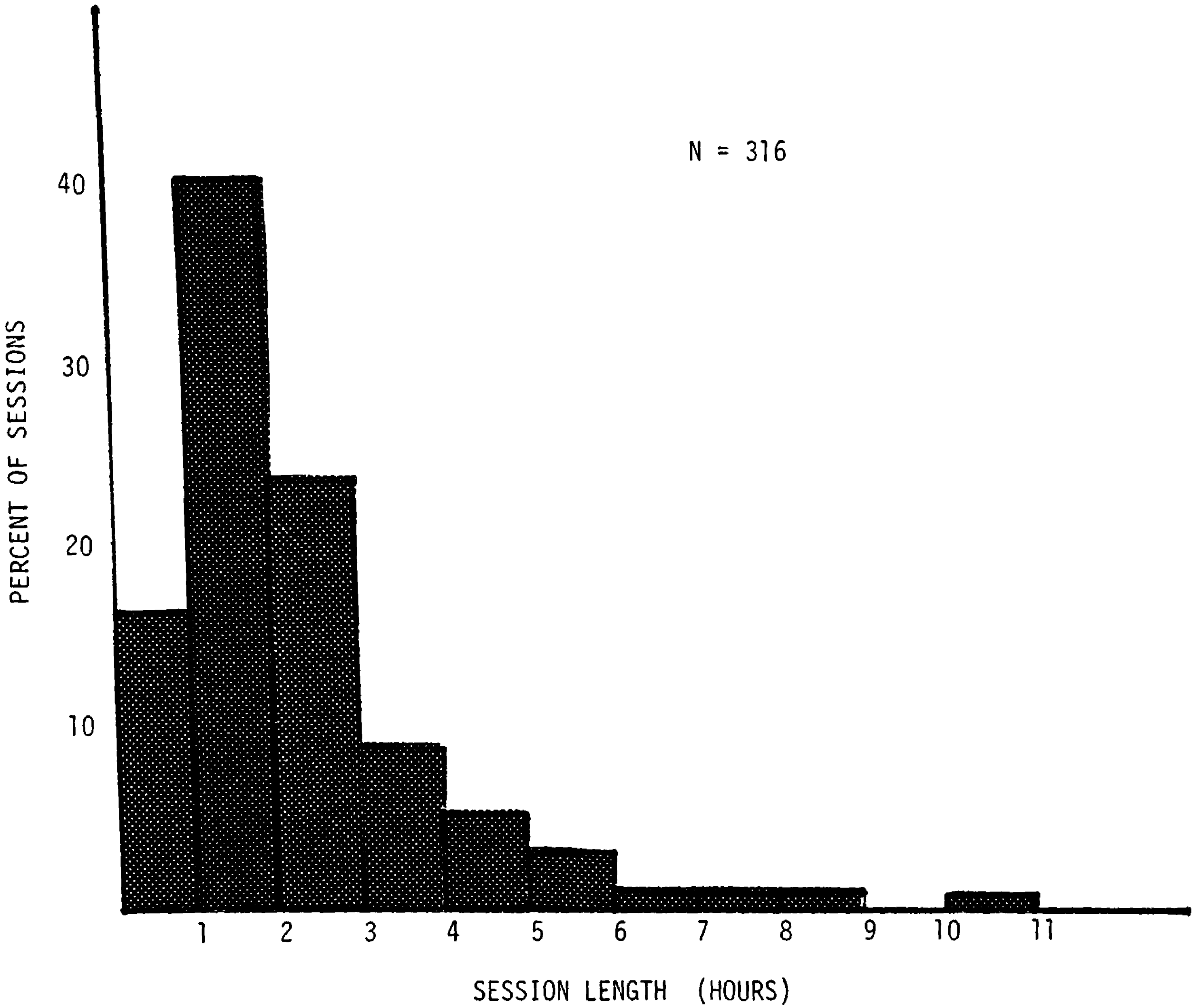


Fig. 4. Frequency distribution of daylight session lengths.

Hatching dates. In 1977, the 15 successful clutches hatched from 14 June to 4 July with the peak activity falling between 14 and 20 June. In 1978, the peak of hatching was between 25 and 29 June, with the last clutch hatching on 13 July. Fig. 5 shows hatching dates for clutches which fledged cygnets and those which suffered total brood mortality; no significant difference in dates existed ($p = 0.05$, Mann-Whitney T test).

Brood size. Mean brood size at hatching was 3.3 cygnets per successful nest (Table 10) and 1.8 cygnets per active nest for both nesting seasons combined. Values were slightly larger in 1977 due to the significantly larger clutches and higher number of successful nests.

Mean brood size at fledging was 2.0 cygnets per brood (Table 11). Actual production to fledging equaled 0.44 cygnets per active nest for 1977 and 1978 combined.

Cygnet mortality. Because the earlier available data on cygnet production in the Tri-state Region came mainly from late August or early September surveys, I calculated comparable production figures for this study, although actual survival to fledging was lower. Survival of cygnets to September was 33% (17 of 52) in 1977 and 29% (10 of 35) in 1978. However, subsequent prefledging mortality in 1977 included two stunted cygnets killed by predators, and a newly fledged cygnet (possibly from nearby "Geode Pond") was shot at a roadside

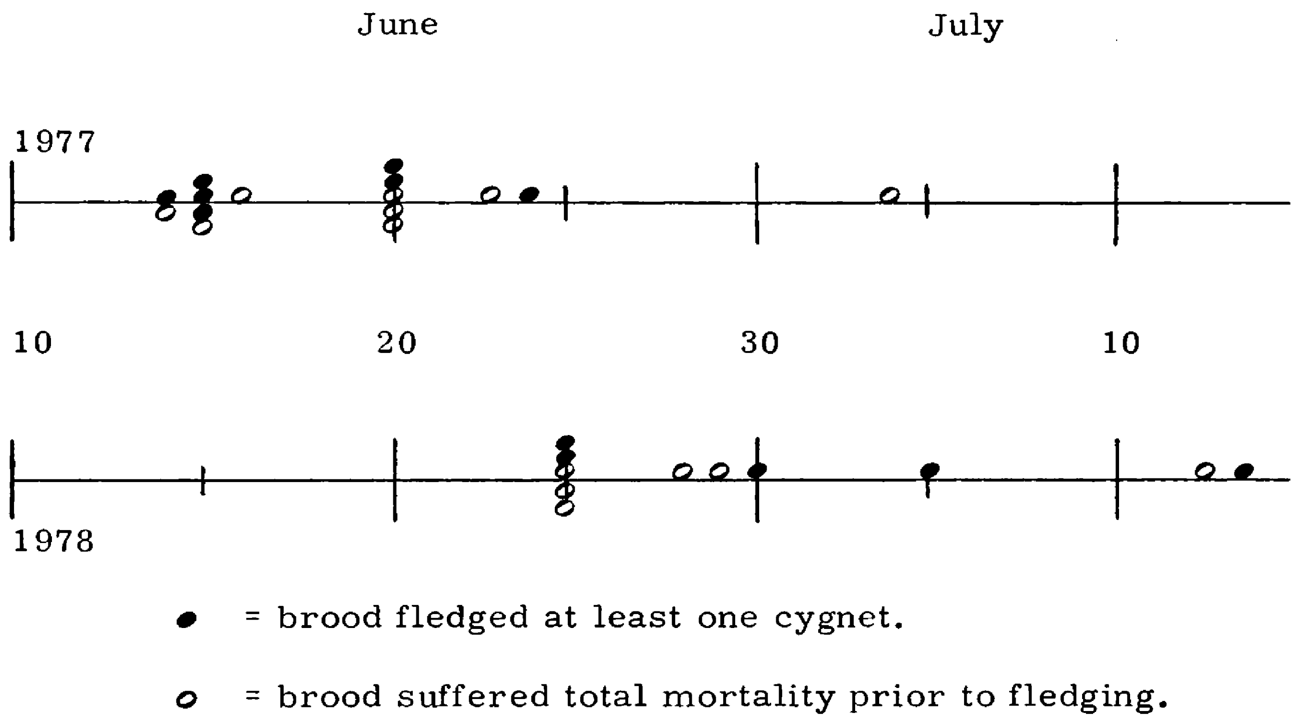


Fig. 5. Hatching dates of Trumpeter broods.

Table 10. Brood sizes at hatching.

	Brood size						Mean cygnets/brood
	1	2	3	4	5	6	
	No. of broods						
1977 n = 15	2	3	3	2	3	2	3.5
1978 n = 11	1	3	2	3	2	0	3.2
Total n = 26	3	6	5	5	5	2	3.3

Table 11. Brood sizes at fledging.

	Brood size						Mean cygnets/brood
	1	2	3	4	5	6	
	No. of broods						
1977 n = 7	3	2	2	0	0	0	1.9
1978 n = 4	2	0	1	1	0	0	2.3
Total n = 11	5	2	3	1	0	0	2.0

pond near Tower Junction. Two other stunted cygnets had little chance of surviving. This known and assumed autumn mortality lowered actual production to 12 cygnets (23%) in 1977. Only one known autumn cygnet death occurred in 1978, leaving nine (26%) surviving to fledge. Cygnet survival for both years combined was 24%.

Of the 65 cygnets which died prior to fledging, 50 (77%) were members of the 15 broods which suffered total mortality. The other 15 cygnets were from the 11 broods that had partial survival.

Of the 52 cygnets that hatched in 1977, 33 (63%) died within 45 days. Initial survival was good with only six cygnets (12%) dying in the first 16 days. Mortality then increased abruptly as 16 cygnets died between days 17 and 26, an entire loss of six of the 15 broods. High mortality continued with 11 more cygnets dying between days 35 and 45 (Fig. 6).

In 1978, 35 cygnets hatched from 11 successful nests but five entire broods died within 2 weeks of hatching. The greatest mortality occurred within the first 10 days of life, when 19 (55%) of the cygnets perished. The further loss of six cygnets between 10 and 90 days of age left 10 cygnets alive on 16 September. Nine of those birds probably fledged. I captured the tenth cygnet and took it to the Veterinary Research and Diagnostic Laboratory in Bozeman, Montana, for observation because it was severely stunted.

The pattern of mortality showed that approximately 65% of the

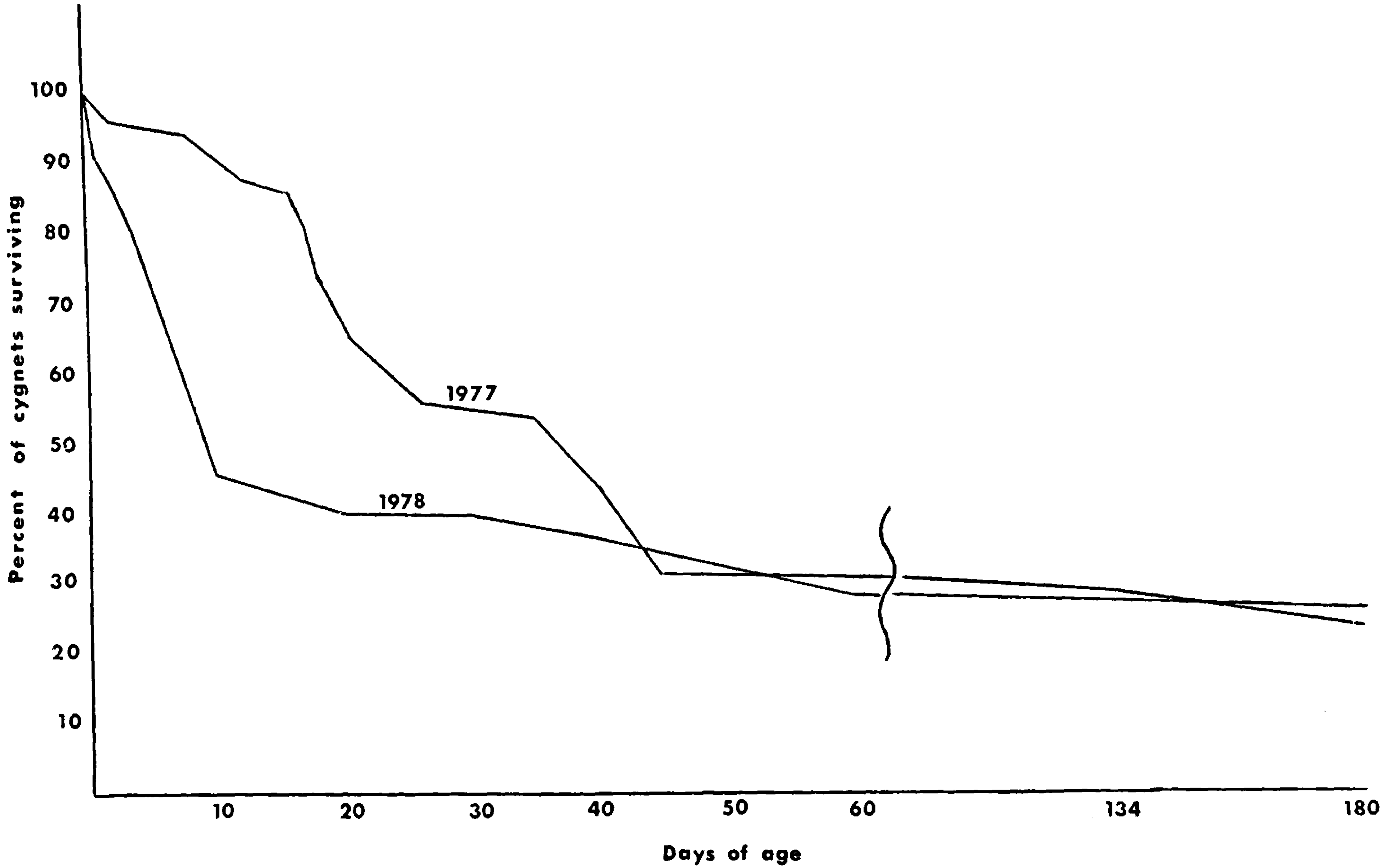


Fig. 6. Cygnet survival.

cygnets were of low viability and predisposed to rapid, total brood mortality within 6 weeks of hatching. The onset of this mortality was delayed about 2 weeks in 1977 as compared to 1978.

Influence of clutch size on cygnet survival. Small clutch size correlated significantly ($p = 0.02$, $X^2 = 5.44$, d.f. = 1) with reduced cygnet survival. Cygnets from clutches of four or fewer eggs ($n = 12$) suffered 90% mortality, with a complete loss of 75% of the broods. In contrast, cygnets from clutches of five or six eggs ($n = 12$) suffered 69% mortality, with a loss of 42% of the broods. Better survival of cygnets from the larger broods was also noted in 1971 at La Creek NWR. Records showed that these broods were from the older and more established parents (Trumpeter Swan Society 1971).

Captive cygnets. In 1978, I removed and hatched one egg from each of two nests in YNP. In each case, the embryo was already vocalizing and the egg hatched within 24 hours of its removal from the nest.

Egg A, from the Cygnet Lake nest, was from a clutch of two eggs; the second was infertile. Because of late melting ice and snow, nest initiation occurred after 1 June and insufficient time remained for cygnet development prior to fall freeze-up of the Lake. In addition, no cygnets have fledged from this territory since 1952. When this egg hatched, the cygnet emerged in a very weak condition and possessed a deformed right foot. The three anterior toes curled backward, forcing the cygnet to walk on the distal end of the tarso-metatarsus.

Egg B was from a clutch of six at the "Madison River #2" nest. Two eggs hatched on 13 July but one cygnet died within hours; the second ultimately fledged. Two eggs were infertile, and the fifth contained a fully developed dead embryo. The egg which I removed from the nest contained a vocalizing embryo. After I assisted it in hatching, the cygnet exhibited shaking of the head and neck and a deformed right leg. The limb was twisted so that the foot turned 90 degrees under the body, thus making terrestrial locomotion difficult.

Both of these deformed cygnets were held in a brooding chamber and treated by J. DeSarro of the Brown Thomas Meadow Ranch, Cody, Wyoming. The deformed limbs were manipulated into normal position and supported with splints. After 1 week of the splint treatment and a diet of a commercial Turkey Starter, both cygnets appeared normal, with no evidence of tremors or deformities. The birds, however, never showed normal vigor and eventually died of aspergillosis.

Seven eggs were taken from a nest at RRNWR in May 1978 and artificially incubated by DeSarro. Two of the five cygnets that hatched had similar deformities. Both birds suffered from a backward curling of the toes of both feet as well as an asymmetry of the neck and rapid shaking of the head. Both died within a few days of hatching. The entire brood was very weak and in the propagator's opinion would have survived no more than a few days in the wild (J. DeSarro personal communication).

Moribund wild cygnets. The two cygnets hatched at Indian Lake (1978) swam adequately when approximately 2 days old but on land they lunged forward using both legs simultaneously in a strenuous hopping motion. Because of the distance of their nesting island from shore, I could not see their feet, but their erratic movements suggested a deformity; they disappeared 2 days later.

At Harlequin Lake (1977), three of the four cygnets died when about 10 days old, and the surviving cygnet swam 10 to 15 meters behind the parents, strenuously shaking its head from side to side. It died within 4 days.

At Aldridge Lake, where the entire clutch of six eggs hatched on 15 June, only four cygnets remained with the parents 17 days later. A fifth live cygnet was found lying on a mud flat 3 m from the water. The bird was very weak but showed no sign of injury or deformity. It could move all extremities but made no voluntary movements when placed in shallow water. It had difficulty holding its neck erect and occasionally flicked its head rapidly from side to side. Death occurred within 3 hours.

The symptoms of the captive cygnets were consistent with the temporal pattern of mortality observed in the wild and the frequent rapid disappearance of entire broods. The deformed cygnets were able to swim but were virtually helpless on land. Unless forcibly corrected, the deformities became progressively more severe and would have predisposed the cygnets to death in the wild within the first few weeks of life. The foot deformities were not always obvious after death and rigor mortis occurred. I suspect that several of the wild broods I observed swimming, but which disappeared entirely within the first few weeks, suffered similar problems, although this was not apparent when carcasses were retrieved.

Past production in YNP. The production histories of territories in YNP from 1931 to 1978 were reconstructed using information from YNP files. These data showed that certain territories exhibited consistent patterns of reproductive performance in recent years.

Of the YNP territories where total brood mortality occurred during the study ("Trail Creek Pond," "Calf Creek Pond," "Little Robinson Pond," "Bunsen Peak Pond," Cygnet, Harlequin, and "Trumpeter" lakes), none have fledged cygnets since 1968. They have fledged a combined total of only one cygnet since 1955. During the study, these territories hatched and lost 31 cygnets. Average hatching success, followed by total brood mortality has probably been chronic in this group in recent years. Historically, these areas were much more productive; between 1931 and 1954 they fledged at least 97 cygnets.

The nine YNP nests that failed to hatch any eggs during the study showed a different long-term pattern of production. Two of these sites ("Delta North" and "Richards Creek Pond") had no previous record of nesting. The remaining seven sites have each fledged young since 1963. Three territories fledged young in either 1974 or 1975, though none have produced since. Since 1960, when the overall decline in production became evident, these seven areas fledged 33 cygnets. Successful hatching may be more sporadic at these territories but cygnet mortality, although high, is not usually total.

A small number of territories consistently fledged cygnets. Of the 31 territories used in 1977 and 1978, only 12 fledged young. Four sites (Thompson Hole, Madison River, Aldridge and Riddle lakes) produced 69 and 56% of the cygnets which fledged in 1977 and 1978, respectively. The remaining 44% of the 1978 production came from Chain Lake, a territory not studied in 1977.

A reconstruction of past production in YNP (Table 12) shows constant or increasing production from the 1930's to 1950's followed by a sizeable decline beginning around 1960 and continuing to the present. The survival both of fewer broods and fewer cygnets per brood characterized the decline. Little historic information on brood sizes at hatching was available but the few existing observations suggested that cygnet survival to fledging was much higher in the 1930's than at present. The present number of nesting pairs exceeds the number found in earlier years so a reduction in the number of nesting pairs certainly is not the cause of lowered production.

The high cygnet mortality observed in 1977 and 1978 has probably been occurring for almost 20 years.

Survey dates varied from 16 July (1952) to 28 September (1961) but usually have occurred after mid-August, when subsequent cygnet mortality would have been small.

Table 12. Average (range) annual cygnet production per decade in YNP.*

	Cygnets produced	Cygnets fledged per brood	Broods fledged	% cygnet survival
1930's	11.8 (2-29)	3.1 (1-7)	3.7 (1-8)	73
1940's	12.9 (8-21)	2.6 (1-5)	4.8 (3-6)	...
1950's	13.3 (9-23)	2.7 (1-6)	4.9 (3-7)	...
1960's	6.1 (2-12)	2.1 (1-6)	3.0 (2-4)	...
1970's	4.0 (1-9)	1.7 (1-3)	2.4 (1-5)	24

*Historic data gathered from NPS ranger reports and USFWS aerial surveys.

Cygnet development. In the two years combined, six (22%) of the 27 cygnets that survived until September were slow to develop. Five of the 17 cygnets alive in September 1977 were abnormally small. One of these was killed on 16 September at "Geode Pond" by a predator. When killed, its primaries had erupted less than 13 cm. Its two fully developed siblings disappeared from the Pond in early October. They may have joined with a passing group of migrant Trumpeters and abandoned their parents who remained on the territory with their two stunted cygnets. When last seen on 22 October, these 134-day-old cygnets were still flightless although apparently fully feathered. They probably perished soon after as neither they nor the adults returned to the nesting area the following spring.

At Aldridge Lake on 18 September 1977, two of the three surviving cygnets were conspicuously small and flightless at 105 days of age. The smallest was still downy, with little primary development. During the second week of November the parents flew from the Lake with the two largest cygnets and abandoned the flightless runt. It was killed within 3 days by a coyote.

In 1978, one of the 10 cygnets alive in September was also a runt. This cygnet, the sole survivor of the Aldridge Lake brood of four, was captured on 19 October. Although 111 days old, it weighed only 4.25 kg and was still downy on the back, base of tail, and wing coverts. Flight feathers had erupted only 18 cm. This bird was taken to the Veterinary Diagnostic Laboratory in Bozeman and raised in captivity. Blood samples were taken upon arrival and periodically thereafter. Hematology showed the bird was anemic when captured (D. Gullehon personal communication). The cygnet survived in captivity, attaining full primary and secondary feather development by 7 December and reaching a weight of 6.2 kg by 1 February.

Necropsies. The carcasses of nine wild cygnets were recovered intact shortly after death, and frozen until they could be transported for necropsy. All were less than 3 weeks old at death. Three of the cygnets died within hours of hatching and the carcasses were found in the nests or in the water nearby.

Two necropsies were performed at the National Fish and Wildlife Health Laboratory, Madison, Wisconsin; the others were performed at the Veterinary Diagnostic Laboratory, Bozeman, Montana. Diagnosis was inconclusive in each case. No significant bacterial or fungal growth was obtained, and no lesions or internal abnormalities were found. The Aldridge Lake cygnet, retrieved hours before death, showed a small amount of hemorrhage in the lungs, but the primary cause of death could not be determined as stress during handling may have caused the hemorrhage (S. Kerr personal communication). Two cygnets were tested and found negative for avian influenza and New Castle disease. No parasites were found in eight of the cygnets. The ninth cygnet, from Harlequin Lake, suffered severe obstruction of the nares and turbinates caused by two leeches (Theromyzon spp.) which probably hastened death.

Preflight movements. Several families made overland walks of up to 3 km. In at least three cases, the parents tried to lead their brood from the nesting lake to other nearby waters when the cygnets were less than 2 weeks old. Two moves were successfully completed but in both cases the cygnets died within 2 weeks.

At Harlequin Lake, one adult led the four 5-day-old cygnets through the lodgepole pine (Pinus contorta) forest toward the Madison River; the other adult remained behind feeding on the Lake during the episode. On a steep slope, the cygnets became entangled in a maze of fallen timber and could follow the adult no further. The adult began honking and turned back toward the Lake. After approximately 5 minutes of struggling, all four cygnets freed themselves and followed the adult back to the Lake. The entire journey covered about 300 m. Within 3 weeks this brood was dead.

Two families (from "Geode Pond" and Thompson Hole) may have saved their cygnets by traveling overland. Thompson Hole dried up in July 1977, leaving the adults and three cygnets sitting on a bare mud flat. Within the next week the family walked 3 km to Steele Lake where the cygnets fledged successfully. At "Geode Pond" the parents led the four surviving cygnets 1 km to Geode Lake shortly after the fifth cygnet was killed by a predator. Two weeks later, the family walked back to the original pond.

The first overland move of the "Trumpeter Lake" family was in direct response to the presence of a determined photographer. While the man stood on the lakeshore the parents left the lake with the four 4-day-old cygnets and walked some 100 m to "Little Trumpeter Lake." They traveled single file with one adult leading and one following the group. Although the nesting lake provided tall Scirpus stands which would have concealed the whole family, they moved to a pond only one fourth as large and which provided no vegetative cover or islands for security. Several days later they were observed returning to this same pond from the direction of a third pond 1 km distant (M. Law personal communication) but they never returned to the nesting lake and within 3 weeks all four cygnets died.

The activities of an otter (Lutra canadensis) family in these ponds may have encouraged the swans to move frequently.

Interspecific behavior. Trumpeters showed aggression at the nest sites toward Canada Geese, Ravens, moose (Alces alces), muskrat, beaver, and humans. One incubating female chased away a moose which wandered too close to the nest. On another occasion, this same female allowed a pair of Green-winged Teal (Anas crecca) to climb onto the nest while she fed nearby. The male duck walked over to the eggs and began poking as if to turn them while the swans watched and continued to feed.

Geese and ducks commonly fed among the wintering flocks of swans. Usually they were ignored but occasionally they were suddenly attacked with a hard peck of the bill.

Predation. In addition to causing the deaths of the incubating females at the 1976 "Beach Springs Lagoon" and 1978 "Delta North" nests, an unknown predator killed a 98-day-old cygnet at "Geode Pond" in 1978. The carcass showed no sign of previous ill health or injury although the bird was slightly retarded in development. Evidence suggested that either a mink (*Mustela vison*) or an otter was involved in the attack.

Many of the small cygnets disappeared without a trace and predation may have been involved in some losses. However, no harassment of swans by potential predators was observed and none of the carcasses which I retrieved had been touched by predators or scavengers. In several cases, abandoned and exposed eggs remained intact for weeks, unmolested by other animals.

Black bear (*Ursus americanus*), grizzly bear (*U. arctos*), coyotes, lynx (*Lynx canadensis*), Bald Eagles (*Haliaeetus leucocephalus*), Golden Eagles (*Aquila chrysaetos*), and Great Horned Owls

(*Bubo virginianus*) were observed in the study area. Low numbers of cougar (*Felis concolor*), bobcat (*Lynx rufus*), striped skunks (*Mephitis mephitis*), red fox (*Vulpes vulpes*), and raccoons (*Procyon lotor*) also occurred around nesting lakes. Any of the above species might prey effectively on Trumpeters.

Color phases. Most cygnets are pale grey when hatched and retain the grey plumage through their first winter. About 13% of the cygnets hatched in YNP in the 1930's were white (Condon 1941), although the phase had been noted only once in the Park since that time. These were not albinos but rather "leucistic" individuals. Scott (1972) discussed the genetics of this color phase in the Mute Swan (*Cygnus olor*).

Recent records of leucistic Trumpeters come from the Yellowstone River delta in 1968 (USFWS swan survey 1968), from South Dakota in 1974 and 1975 (Trumpeter Swan Society 1976) and from Wolf Lake, near Grande Prairie, Alberta, Canada, in 1958 (correspondence from R. MacKay to D. L. Condon, YNP files).

I observed a leucistic adult in 1977 at Harriman State Park among a flock of normal Trumpeters. This bird had pale yellow legs, dark eyes, and symmetrical bright yellow marks on the lores. Its bill coloration resembled that of a distinctly marked Whistling Swan.

During the 1978 nesting season, two white and two gray cygnets fledged from a nest in the Targhee National Forest. During September, these cygnets had white feathers, pale yellow legs, and flesh-colored bills with pale grey base and nail. In October 1978, two normal adults arrived at Yellowstone Lake with a single leucistic cygnet. No grey was visible on its flesh-colored bill, indicating that this was not one of the two white cygnets fledged in the study area.

In December 1978 two normal adults were observed at Harriman State Park accompanied by one gray and one white cygnet. Two adults with a single white cygnet were reported on 21 January 1979 a few miles south and west of YNP's south entrance (J. Weaver personal communication).

Dispersal. Most swans remained on their territories from their arrival in spring until September when pairs without cygnets began to gather on the Yellowstone River between Yellowstone Lake and Alum Creek, and on the Madison River below Madison Junction. Families remained on their territories until at least the first week of October. Some pairs remained until the last possible moment, shattering the ice when they finally departed.

Human Disturbance

Activity level and swan productivity. Annual Park visitation rose from under 200,000 persons in 1945 to over 2.6 million persons in 1978 (Fig. 7). Overnight backcountry use amounted to less than 1%

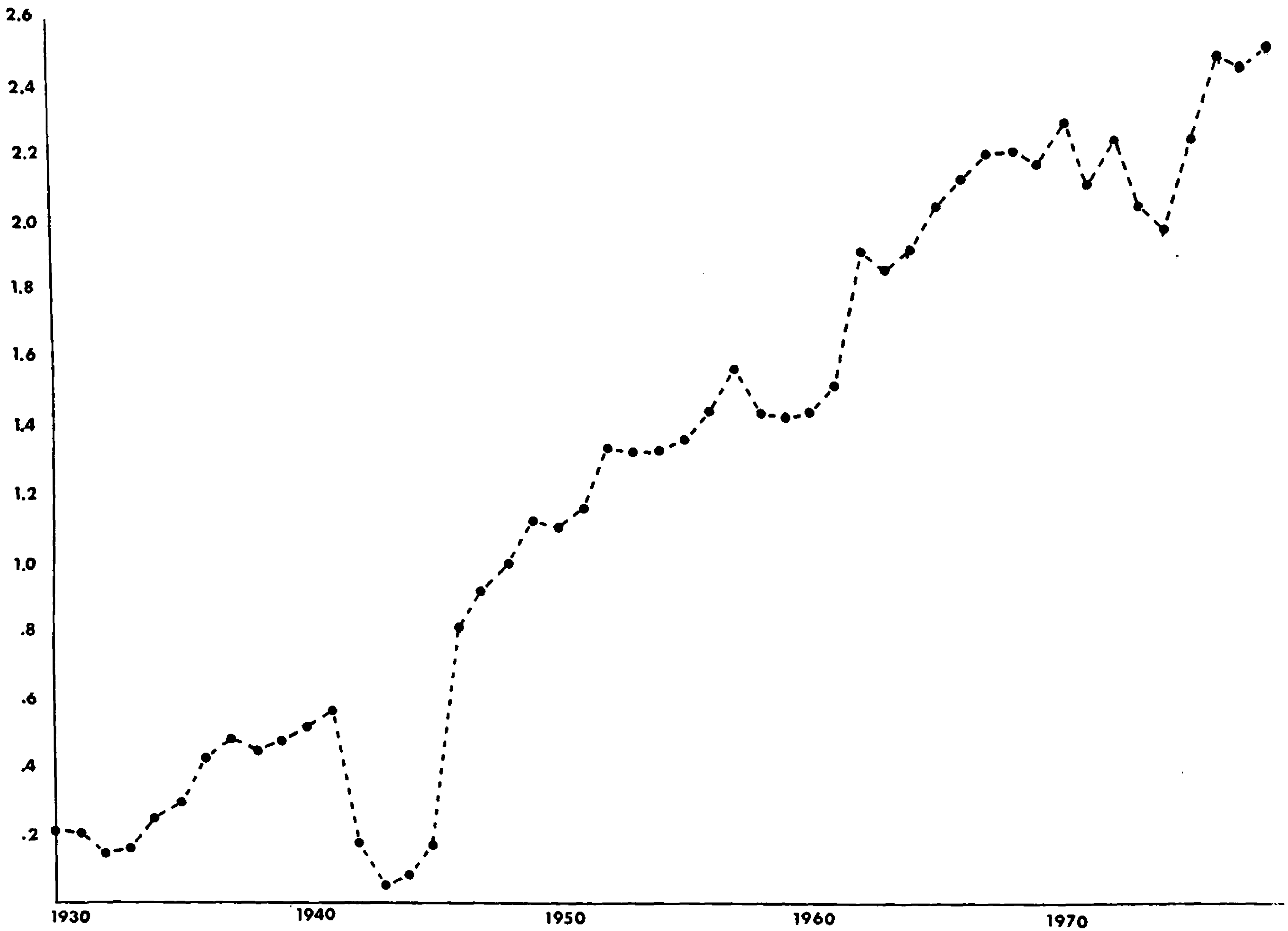


Fig. 7. Millions of visitors to YNP, 1930-1978.

of total visitation but has increased substantially in the last decade (Table 13). April and May backcountry use varied greatly depending on snowpack and weather and concentrated primarily in the lower elevation northern portion of the Park. Activity in these months was slight, totaling about 1000 persons Park-wide (YNP files). By June, backcountry use increased noticeably; 3643 and 3982 persons received backcountry camping permits in 1977 and 1978, respectively (YNP files).

Table 13. Backcountry use in YNP.

Year	Overnight users
1969	6,697
1970	6,786
1971	10,365
1972	12,323
1973	13,833
1974	16,801
1975	17,994
1976	20,245
1977	23,135
1978	21,196

Human access into most roadless portions of the study area was quite difficult until mid-June due to slowly melting snow and streams swollen with runoff. YNP's backcountry permit system provided a valuable method of directing human use away from particular sites. As a result, 17 territories (Group A) received no human visitation until after the cygnets had hatched. At the other 14 territories, human visitation varied from about two persons ("Bunsen Peak Pond") to several hundred persons per week during incubation and brood rearing periods.

Cygnet productivity per active nest did not differ significantly between the two groups (Table 14). However, the number of active nests per territory in 1977 and 1978 differed significantly ($p = 0.05$, $X^2 = 4.59$, d.f. = 1) between groups, being 0.91 and 0.69 at undisturbed and disturbed territories, respectively. Swans were more likely to occupy a territory without nesting or to be absent entirely 1 year out of 2 at locations where human activity occurred. Swans that could tolerate the high human activity levels moved in and pioneered two sites following the previous residents' deaths ("Beach Spring Lagoon" and Swan Lake, Idaho). The effects of disturbance were subtle, causing a significant reduction in nesting effort rather than a reduction in cygnet production per nesting attempt. However, the latter could easily have occurred at several nests had certain events coincided, and nesting attempts likely have been destroyed by human activity in past years.

Major disturbance occurred at certain lakes in YNP. Both Grebe Lake and "Beach Springs Lagoon" were among the historically most productive Trumpeter territories in the Park (Appendix A). In spring, however, neither lake has significant emergent vegetation or an island. Consequently, the swans historically nested on shore or in shallow water close to shore where they were extremely vulnerable to disturbance.

Table 14. Cygnet production and nest establishment at undisturbed (Group A) and disturbed (Group B) territories.

	Group A	Group B
Cygnets hatched/active nest	1.6	2.1
Cygnets fledged/active nest	0.44	0.42
% survival to fledging	21%	27%
Nest established/territory per year	0.91	0.69

Grebe Lake attracted day hikers, fishermen, and overnight campers throughout the summer with regular visitation beginning in May. There were 10 to 15 persons present at the 63 ha lake each time I visited it. A fisherman's trail followed the shoreline and no secure nesting site remained. Swans used the Lake both in 1977 and 1978, but made no effort to nest. This pair did not fear humans; they begged for handouts and walked into campsites in the evening, searching for food. Reconstructing how many years have passed since swans nested at Grebe Lake was impossible, but it has been 26 years since cygnets fledged there.

A similar problem existed at "Beach Springs Lagoon" where visitors walked to the lake from the adjacent road. Because of a slight ridge, the nesting site was not visible to the occupants of cars, and the swans usually remained hidden from most passing traffic. A small group of bison stayed near the pond, however, and visitors often discovered the nesting swans as they approached to photograph the bison.

In 1978, swans nested there for the first time since 1976 when one of the nesting adults was killed by a predator. The nest was less than 1 m from the shore nearest to the road and quite vulnerable to egg robbing or vandalism, as well as unintentional disturbance.

Due to the prevailing winds off Yellowstone Lake the swans are most likely to continue nesting in the slight shelter of the ridge nearest the road. Human disturbance, however, did not destroy the 1978 nesting attempt; the female laid only one egg and it was infertile.

Although several factors may have contributed to the recent low productivity of these two sites, the complete vulnerability of the nesting sites to human interference makes successful nesting unlikely even if the other factors are corrected.

Reaction of swans to humans. Individual Trumpeters varied greatly in their response to humans. Generally, swans that regularly saw humans in their territories accepted the human presence with little observable response as long as the humans did not make a direct advance. At Swan Lake along U.S. Highway 191 near Last Chance, Idaho, and on the Madison River in YNP, incubating Trumpeters showed no concern as heavy traffic passed within 200 m of the nests. When humans stopped to watch the swans and emerged from their vehicles, the incubating birds only raised their necks stiffly in alert postures, if they responded at all. As long as a nest was on a secure site with a protective expanse of water between the nest and the road, the swan virtually ignored passing humans.

Swans that habituated to people showed little fear even when threatened. During early incubation, the female at "Beach Springs Lagoon" slowly left the nest when approached by humans. After about the third week she stood and assumed a defensive posture on the nest. If humans arrived while she was out on the lake feeding, she quickly swam to the nest to defend her clutch. Twice I observed the male join her and move to the nest. One day late in incubation, two large men stood less than 3 m from the nest for at least 5 minutes. The distraught swan stood on the nest with wings partially extended and quivering, hissing continuously and ready to attack. She settled on the clutch as soon as the men turned and began walking away. I later visited the nest to determine the fate of unhatched eggs while the swans were off feeding nearby. One of the adults swam to the nest and defended it vigorously, attempted to hit me with its wing and chased me some 30 m toward the road. The object of this effective defense was one broken and very rotten egg.

Most nesting swans, however, reacted immediately to humans by slipping quickly off the nest and swimming away from the intruder. Often the reaction occurred at the first sight of the human even though he was on the far side of the lake. Once off the nest, the swans showed little further sign of alarm, often feeding leisurely, but they would not return to the nest and resume incubation until the person left. If deliberately approached, the swans gave low honks of alarm and swam away if possible. On four occasions when the approach continued, they eventually flew from the lake. Occasionally, to escape detection, a swan stretched its head and neck out flat on the water, minimizing its visibility as it sought cover among the emergent vegetation. Even though they saw at least five persons per week throughout incubation, the Aldridge and Riddle lake swans left the nest each time a person appeared, and did not habituate to human presence.

Without exception in over 50 observations, when a swan left the nest to feed she took 3 to 5 minutes to cover the clutch with loose dry vegetation. When disturbed by humans, however, the female never delayed to cover the eggs before departing. Thus a recess initiated by disturbance has a much greater chance of harming the eggs than a normal feeding recess.

Swans also varied greatly in their defense of broods. At remote sites, the adults usually abandoned the brood if a human persisted in efforts to approach them. The parents either swam or flew to the far end of the lake, leaving the cygnets to follow. In contrast, the Madison River families often fed within 20 m of the road even though more isolated backwaters of the River were available.

Disturbance of wintering swans. Wintering flocks also varied in their reaction to humans. The 30 swans on the Madison River between Madison Junction and West Yellowstone, Montana, wintered within 50 m of the road and heavy snowmobile traffic from December to March. When visitors stopped the swans often retreated slowly to the far side of the River but continued to feed without alarm.

Trumpeters on the Yellowstone River flew if surprised by a person's sudden appearance, but usually swam out of sight around a bend in the River if they saw the person coming. Swans on Yellowstone Lake rarely flew when they had the option of merely swimming further out from shore, but when flushed from a site, they were not likely to return, as was the case at Pelican Creek in 1977.

The large wintering flocks at Harriman State Park showed a more pronounced reaction to humans. Approach by a person on skiis or snowmobile was sufficient to put scores of birds into flight. They often moved several km to another stretch of river. The few swans which stayed near the highway were slightly more tolerant of human contact and usually just swam away from the intruder, but eventually flew if contact persisted.

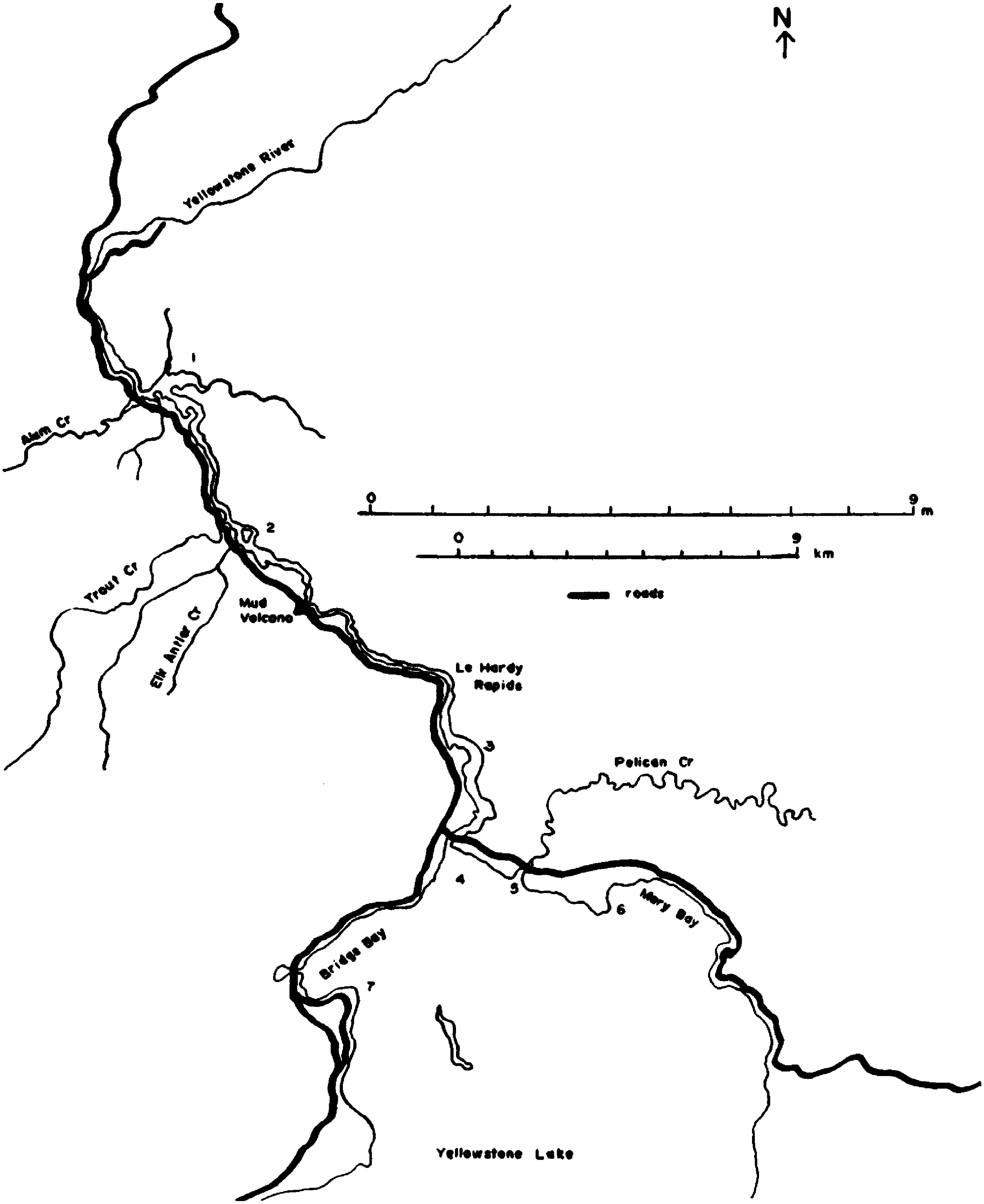
Fall Migration and Wintering

Arrival. The first migrant Trumpeters appeared on the Yellowstone River (Fig. 8, sites 1, 2, and 3) between 14 and 20 October in 1976, 1977, and 1978.

Adults, and/or subadults, usually in groups of three to eight, arrived first. Most family groups appeared 2 or more weeks later. Less than a dozen cygnets were present in any year until about 30 October when their numbers rapidly began to increase.

Maximum counts of Trumpeters. The peak of migration occurred during the second week of November with between 265 and 312 Trumpeters present. The highest counts occurred in 1977. Maximum counts for 1976 and 1978 were quite similar (Table 15), although swans were still arriving on 9 November 1978 when a severe storm curtailed censusing until 16 November. Another snowstorm on that date terminated access to the study area for the year.

Trumpeters also used remote portions of YNP that could not be censused regularly. Aerial observers found swans on Riddle Lake, Shoshone Lake, the Madison River between Madison Junction and West Yellowstone, and the south and southeast arms of Yellowstone Lake. Use of these areas was limited to between 5 and 20 swans except for the southern arms of Yellowstone Lake where 40 to 75 were observed (D. Stradley personal communication). Over 130 swans used the


N
Yellowstone River
1
Alum Cr
2
Trout Cr
Elk Antler Cr
Mud
Volcano
0
9
m
0
9
km
roads
Le Hardy
Rapids
3
Pelican Cr
4
5
6
Mary Bay
Bridge Bay
7
Yellowstone Lake

southern arms in November 1978 and orange neck-banded birds were seen on several occasions. Whistling Swans were rare in the study area at that time and it is likely that most of those swans were Trumpeters.

Table 15. Maximum counts of Trumpeters in the Yellowstone Lake vicinity, 1976-78.

	1976		1977		1978	
	Date	Number	Date	Number	Date	Number
Adults	11/15	221	11/10	254	11/8	220
Cygnets	11/24	52	11/9	74	11/16	52
Maximum	11/15	265	11/9	312	11/8	266

Marked Trumpeters. Neck-banded Trumpeters from Grande Prairie, Alberta, visited YNP each autumn. Neck-bands were either yellow with a four-unit alpha-numeric code or orange with a two-unit code; they were easily visible through 7x35 binoculars. A 40x spotting scope was needed to read the neck-band codes. A total of 69 different neck-banded Trumpeters were located at Yellowstone Lake. Including unmarked mates and cygnets, these accounted for over 50% of the known Grande Prairie summer population.

Considerable site fidelity among marked birds was noted. Of the 50 neck-banded Trumpeters observed at Yellowstone Lake in either 1976 or 1977, 25 returned and were resighted the following year. Of the 25 that failed to return, 20 were cygnets which may have suffered high mortality during their first year of life. Six of the 16 neck-banded adults found in 1976 returned to the same locale both in 1977 and 1978.

Marked adults commonly used the same stretches of river each autumn, often loafing on the same sandbar year after year. In two instances, marked yearlings returned alone to the same site where their parents had brought them the previous autumn. The same marked Trumpeters moved to Hebgen Lake each year and the same parents brought their marked cygnets back from Idaho to the Yellowstone River each year in February. Some families appeared to possess rather rigid migratory patterns which were taught to the cygnets and maintained by the offspring after they were independent.

Estimated total use. In 1976, all neck-banded Trumpeters remained in the study area until at least 5 December when observations ended. Sightings of these marked swans and of other recognizable family groups indicated that very little movement of Trumpeters through the area occurred from October to December. The maximum adult and cygnet counts showed that a minimum of 273 migrants visited the study area. Including Trumpeters that utilized the southern portions of Yellowstone Lake and the few individuals that were not present on the days of maximum counts, I estimated that 300 to 325

Trumpeters used the Park in 1976.

On 9 November 1977 when the maximum number of Trumpeters (312) were censused, 30 neck-banded birds were present. This represented only two-thirds of the 45 neck-banded Trumpeters observed at Yellowstone Lake between 14 October and 12 December. Dividing 312 by two-thirds yielded an estimate of 468 Trumpeters using the area in 1977. That estimate was based on the conservative assumption that all Trumpeters present in the area were found on the 9 November census and did not include swans that occupied other inaccessible portions of YNP.

During 1978, a minimum of 220 adult and 52 cygnet Trumpeters visited the study area. In addition, use of the south and southeast arms of Yellowstone Lake was greater than in the previous 2 years. The cessation of regular censusing on 9 November because of heavy snow precluded an estimate of total swan numbers.

Brood size and cygnet percentage. Mean brood size was calculated each year on the day when maximum cygnet numbers occurred (Table 16). Although some families that passed rapidly through the area were missed, most recognizable families were present. Yearly variation in brood size was not statistically significant ($p = 0.05$, $F = 1.49$, $v_1 = 2.0$, $v_2 = 57.0$), however, the larger brood size in 1977 corresponded to record cygnet production in the Grande

Prairie region. The mean brood size of 3.0 (n = 59) was 50% greater than the mean size of 11 broods fledged in the study area (2.0). The percent of cygnets in the migratory flocks each year during November averaged 21.1% (Table 17) and was slightly higher than the percentage of cygnets counted during the February Tri-state aerial surveys.

Table 16. Brood sizes during migration.

	Brood size						Mean	Date of count
	1	2	3	4	5	6		
	No. of broods							
1976	5	5	4	1	3	1	2.7	11/24
1977	2	3	7	6	3	1	3.4	11/9
1978	4	3	6	6	0	0	2.7	11/16
Total	11	11	17	13	6	2	3.0	

Table 17. Percentages of cygnets in flock.

	Yellowstone Lake	Mid-winter Tri-state counts
1976-77	19.6%	17.5%
1977-78	23.7%	20.5%
1978-79	19.5%	14.2%
All years	21.1%	17.4%

Length of stay. In 1976, all marked Trumpeters remained at Yellowstone Lake until at least 5 December when censusing ended. The mean minimum length of stay was 38 days for adults (n = 11) and 22 days for families (n = 3), reflecting the later arrival of families.

In 1977, Trumpeters showed a greater tendency to leave the study area before freezing occurred. During the 57-day observation period ending on 10 December, the mean minimum length of stay was 34.3 days for paired adults without broods (n = 11), 29.8 days for unpaired adults (n = 5), and 12.1 days for families (n = 11). In addition to their later arrival, five families remained for 3 days or less, while only three other adults stayed for less than 20 days.

Length of stay could not be calculated for 1978 because of the early termination of censusing.

Site preference. Although the primary area used by migrant Trumpeters encompassed 32 km of river and lakeshore, use concentrated at seven sites each year (Fig. 1). These sites totaled 12.8 km of river and lakeshore; only very limited feeding or loafing activity occurred outside the sites.

In October and early November, swans primarily used areas 1, 2, 3, and 5. Area 5, a sand spit at the mouth of Pelican Creek, was used on sunny afternoons by up to 125 swans. As ice accumulated in the River and along the northern lakeshore in mid- to late-November, swans shifted their activity to areas 3, 6, and 7, where open water and protection from prevailing southwesterly winds were available. The lower recorded use at area 6 in 1978 (Table 18) probably reflects the cessation of censusing before significant freezing had moved swans into this site.

Table 18. Site use by migrant swans.

Site	% of total use		
	1976	1977	1978
1. Alum Creek area	5	7	10
2. Trout-Elk Antler Creek area	17	12	14
3. 3 km north of Lake Outlet	25	22	43
4. Lake Outlet	16	14	10
5. Pelican Creek Outlet	18	3	11
6. Storm Point	14	34	9
7. Bridge Bay-Gull Point	2	8	2

Two large midstream islands at area 3 provided secure loafing sites close to a popular feeding area and held 30 to 100 Trumpeters daily throughout November. This was the most highly preferred site in 1976 and 1978.

On 25 October 1977, two fishermen walked out onto the sand spit at Pelican Creek (area 5), frightening away about 25 Trumpeters. Although regular use occurred prior to this incident, the swans abandoned this site for the remainder of 1977. Use shifted 3 km eastward to area 6 where a mud flat and dense aquatic vegetation attracted 100 to 120 Trumpeters throughout November and early December.

Movements out of YNP. In December 1977, as Yellowstone Lake and River gradually froze, most swans departed to the south and west, moving 80 km to the Henry's Fork of the Snake River near Island Park, Idaho. Here they joined with other Trumpeters that had been gathering in this area since early November (R. Sandow personal communication). A few marked swans stopped off at Hebgen Lake, Montana, en route to the Henry's Fork, and about 50 Trumpeters moved to the Teton River near Driggs, Idaho (Lat. 43°40', Long. 111°10'). Scattered individuals also used the Island Park Reservoir, Buffalo River, and Madison River near Ennis, Montana (Lat. 45°15', Long. 111°40'). Although at least eight neck-banded Trumpeters wintered at RRNWR in 1977-78 and 1978-79 (R. Sjostrom personal communication), there was no evidence of movement to the Refuge from YNP.

Harriman State Park was unique in its importance as a wintering area for the self-sufficient migratory segment of the mid-continental population. Particularly in December and January, when the winter's coldest temperatures greatly reduced the availability of open water elsewhere, swans concentrated there. In January of both 1978 and 1979, 598 swans were counted in the vicinity of the Park

(Idaho Game and Fish aerial surveys) (Appendix F). No other site in the Tri-state Region supported such a number or density of wintering swans on native vegetation. RRNWR, where between 200 and 300 Trumpeters usually winter, lacks available aquatic vegetation and personnel distribute feed to artificially sustain the swans.

Neck-band sightings showed that Harriman State Park attracted a disproportionately high number of the Canadian swans; very few visited RRNWR. I located 50 neck-banded Trumpeters at Harriman State Park during the winter of 1977-78; 33 of these came via YNP. Of the 15 family groups marked in Grande Prairie during September 1977, 14 were relocated in the Tri-state Region the following winter. One visited RRNWR, 11 were found in YNP, 10 at Harriman State Park, and 9 at both of the latter two locations.

Increased movement through YNP occurred in November 1978. At least 10 marked Trumpeters moved through Grand Teton National Park (J. Weaver personal communication) and remained for only a few days before continuing to an undetermined destination.

As warmer temperatures increased the amount of open water throughout the region, the swans dispersed from the Henry's Fork. The 1979 USFWS Tri-state Survey was delayed until 25 February by inclement weather and found that the swans had dispersed, with a shift of wintering birds to RRNWR and YNP. At least 80 Trumpeters moved onto the Yellowstone River by 13 March 1979.

Aquatic plants. Examination of sites 3 and 6 showed that at these most preferred feeding areas *Elodea canadensis* was the dominant plant species. At site 6 dense beds of *Elodea* (41% wet weight) mixed with lesser amounts of *Eleocharis* spp. (35% wet weight) and *Potamogeton richardsonii* (21% wet weight) covered the lake bottom for a distance of 300 m from shore. Water depth in October 1977 was only 1 m and provided ideal feeding conditions.

At site 3, dense beds of *Elodea* again dominated the shallow feeding areas. Small quantities of *Ranunculus aquatilis*, *P. richardsonii*, *Callitriche* spp., and *Eleocharis* spp. also occurred. Although these other species may have been used by the swans, only the *Elodea* occurred in sufficient quantity to sustain the 100+ Trumpeters that used the site.

At Harriman State Park, tangled mats of 1 to 2 m long *E. canadensis* and *Myriophyllum exalbescens* blanketed the river bottom. Lesser amounts of *P. richardsonii*, *P. pectinatus*, *R. aquatilis*, *Callitriche* spp., and *Eleocharis* spp. also occurred.

Samples taken in the same general area of the Henry's Fork in October 1958 (Hansen 1959) showed several differences in species composition (Table 19). Variation in sampling sites, and possibly methods, limits the usefulness of detailed comparison between the two surveys. However, the large shift and present dominance of *Elodea* and *Myriophyllum* may indicate an increase in these species, possibly at the expense of the tuberous Potamogetons, Ranunculus aquatilis, Sagittaria spp., and Naias spp.

Table 19. Species composition (wet weight) of aquatic vegetation at Harriman State Park.

	This study	Hansen (1958)
Elodea canadensis	35%	4%
Potamogeton pectinatus	32%	40%
Myriophyllum exalbescens	23%	7%
P. richardsonii	3%	3%
Callitriche sp.	1%	1%
Ranunculus aquatilis	1%	13%
Sagittaria sp.	not found	9%
Naias sp.	not found	16%

Although the exposed vegetative portions of the Potamogeton spp. were beginning to die in October 1977, the tubers showed evidence of heavy utilization by swans. At several locations, characteristic feeding pits bordered with torn plant fragments covered the river bottom. These pits were dug when feeding swans raked the River bottom with their feet in order to dislodge the tubers. Extensive feeding pits also occurred in stretches of river that were devoid of vegetation when examined. Presumably these sites supported Potamogeton beds in the recent past.

Injured swans. No dead birds were found during migration or wintering but several Trumpeters showed evidence of hazardous encounters. One cygnet on the Yellowstone River had its lower mandible badly entangled in monofilament fishing line and a bloodied adult had a treble-hooked fishing lure embedded in its bill.

On four widely separate occasions an adult was observed to have a large knob of dried tissue between its eyes. Close examination of one recently injured bird showed that the horny epidermal covering along the culmen had been ripped away at its nostrils and pushed back into the crown over the bird's eye. Such an injury could have resulted from a collision, perhaps with a wire or power line.

Whistling Swans. Numerous Whistling Swans migrated through the study area in October and November; spring migrants were uncommon. Small groups of 20 to 30 stopped at Yellowstone Lake and usually remained 2 days or less before continuing their autumn flight south. While at Yellowstone Lake they commonly intermingled with the Trumpeters, feeding and loafing side by side.

On at least six occasions, Whistling Swan cygnets were left behind when the flock departed. At least twice, these cygnets joined Trumpeter families and remained closely associated with their adopted families for several weeks.

Maximum counts at Yellowstone Lake were 119 on 9 November 1976, 65 on 7 November 1977, and 21 on 8 November 1978. Whistling Swans were noticeably absent from Yellowstone Lake in 1978; 15 of the 18 censuses recorded 10 or less.

The number of Whistling Swans wintering in the Tri-state Region varied from year to year. Approximately 40% of the swans observed at Harriman State Park in January 1977 were Whistlers (A. Doberstein personal communication) and their presence inflated the 1977 USFWS Winter Trumpeter Survey results. Whistlers made up 50% of the swans on the Teton River and 5% of those on the Henry's Fork in January 1978, and 10% of the swans observed at Harriman State Park in February 1979. Banko (personal communication) believes this represents an increase in the number of wintering Whistling Swans compared to the 1950's.

Mute Swans. In addition to the two native species of swans found in the Tri-state Region, feral Eurasian Mute Swans also nested and wintered there. The Mute Swan population centered near Livingston, Montana (Lat. 45°40', Long. 110°35') where one pair was imported to a private ranch in 1964 (D. Skaar personal communication). Aerial surveys in 1978 located 50 Mute Swans in this area.

On 17 June, the count included three families with 18 cygnets. A follow-up survey on 8 August revealed 100% cygnet survival (D. Stradley personal communication).

Most Mute Swans wintered in the same area; 46 were counted on the Yellowstone River south of Livingston in February 1979 (J.

Phillips personal communication).

All of these swans were free-flying and as far as is known, all feral Mute Swans in Montana derived from the Livingston colony. Since 1972, Mutes have been sighted at Wilsall Reservoir, Three Forks, Canyon Ferry Reservoir, Ennis Lake, and north of Ravalli. The magnitude of nesting dispersal is not known (D. Skaar personal communication).

I observed wintering Mute Swans on Hebgen Lake (1) and at Harriman State Park (4). Two others were reported flying over Mammoth Hot Springs, YNP (J. Mason personal communication). A male Mute Swan, seen at Harriman State Park in January and December 1978 appeared to be paired with a Trumpeter Swan.

CHAPTER V

DISCUSSION

Productivity

The 21 active nesting territories found in YNP during 1977 and 1978 exceeded the number located in any previous year, but this could reflect the intensity of the search rather than a real increase. No detailed search had been made since 1939. The actual number of cygnets fledged, however, was at an all-time low. Census dates varied over the years from mid-July to mid-September, but this variation alone can not account for the recent decrease in recorded production.

Year-to-year variation in the number of cygnets fledged is influenced by several proximate factors. The loss of nests to flooding and infertility, and changes in the mean clutch size were important during this study.

With the peak runoff normally occurring in late May or early June, many Trumpeters were caught midway through incubation, and rising water destroyed their clutches. In years when runoff is unusually slight, such as 1977, the loss to flooding is negligible, and the number of successful nests increases.

Reduction in clutch size during cold, wet springs has been noted in Whistling Swans (Lensink 1973) and in Trumpeter Swans (RRNWR files, Hansen et al. 1971). Johnsgaard (1973) observed that the food available to the breeding females, weather conditions during the egg-laying period, and the percent of young females breeding for the first time also significantly affected clutch sizes. At every territory, clutch size either remained the same, or decreased, in 1978 compared to 1977, but there was no reason to believe that the average age of the breeding females declined in 1978. It is more likely that the late departure of ice from the territories in 1978, coupled with the limited feeding opportunities during the prelaying period, caused the reduction in clutch size.

Loss of cygnets in the first few weeks after hatching appears to be the major cause of low productivity in the Region as a whole, as well as in the study area. Cygnet mortality studies at RRNWR from 1962-1966 found that mortality concentrated during the peak hatching period and the following 4 weeks. Cygnets suffered heavy parasite loads but this was interpreted as the result, not the cause, of their weakened condition. As in this study, the dependence on post-mortem analysis of contaminated, partially decomposed specimens severely limited the findings (Sjostrom 1978).

In some years, such as 1976 when only one cygnet fledged in YNP, mortality must be well over 90%. The prefledging mortality of

76% during this study is comparable to that found at RRNWR. Pre-fledging mortality averaged 72.8% at RRNWR from 1971-73 (Page 1976). In 1969, over 90% of the Refuge's cygnets died within the first 10 days following the hatch (Papike 1970). Vivion (1969) also noted that the heaviest cygnet mortality at RRNWR normally occurred within the first 2 weeks after hatching.

Population Dynamics

Page (1976) analyzed the dynamics of the RRNWR population and concluded that it went through a period of rapid growth from 1935 to 1954 and then entered a period of large fluctuations and slow decline. Both increases and decreases in the population prior to 1954 were density independent. From 1954 to 1973 increases remained density independent, while decreases became density dependent. Banko (1960) also detected the leveling off of the population after 1954, but as Page (1976) pointed out, Banko did not limit the use of mated pairs in his calculations to the known number of nesting pairs. Therefore his conclusions regarding cygnets per mated pair, and broods per mated pair trends were complicated by the inclusion of an unknown number of non-breeding paired swans.

Coinciding with the peak and then slow decline of the Refuge population, a preferred food source, *Elodea canadensis*, declined drastically on the Refuge (Paullin 1973). Page (1976) found evidence that the equilibrium point of the Refuge population decreased after 1966, and pointed out that this drastic reduction of one of the few available spring food plants may be the major cause of the reduced carrying capacity.

The summer USFWS surveys show that the Regional adult population went through a similar pattern of growth from 1931 to 1954, followed by fluctuations from 1955 to 1965 and slow decline from 1965 to the present (Fig. 9). Although the decline in cygnet production began in the YNP area about 1959, the Regional effects were not evident until a few years later when the adult population declined by 22% between 1964 and 1968.

Annual surveys ceased in 1968 and one cannot determine whether the decline continued from 1968 to 1970. The 1971 census, however, exactly duplicated the 1968 adult count. Since 1968, the adult population has appeared relatively stable, suggesting the attainment of a new equilibrium, although gaps in the census data could mask fluctuations. The most recent census (1977) found a 9% decrease in adults from the previous (1974) census.

I estimate that the present Tri-state breeding population consists of at least 90 nesting pairs. This estimate includes an average of 45 nests at RRNWR, 27 in the Yellowstone study area, and at least 20 scattered through Grand Teton National Park, the Bridger-Teton National Forest, and lands adjacent to RRNWR.

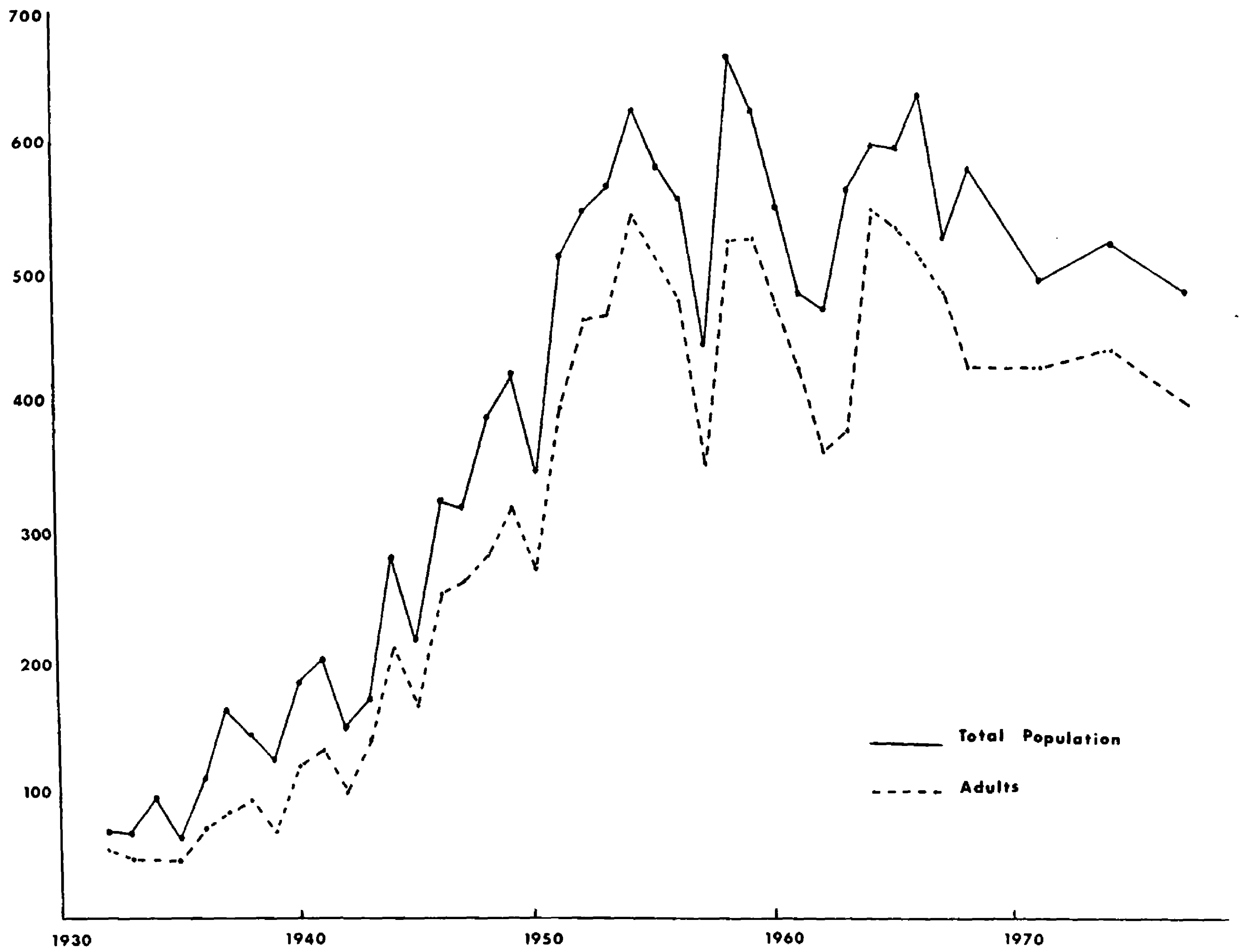


Fig. 9. Tri-state Trumpeter Swan population levels, total and adults only.

Assuming there have been at least 90 nests each year since the adult population peaked in 1964, cygnet production during the last 8 censused years has averaged 0.94 cygnets fledged per active nest. In the study area during 1977 and 1978, only 0.44 cygnets were fledged per active nest.

Turner and MacKay (1978) calculated survival rates for the Grande Prairie Trumpeters based on neck-banding data. Age-specific survival rates were 0.429 for fledging to age 1, 0.709 for age 1 to age 2, and 0.824 for each subsequent age class. If post-fledging survival rates in the Tri-state Region approximate those of the Grande Prairie Trumpeters, then, at the post-1964 level of cygnet production, the typical breeding pair in the Tri-state Region will require 10.3 breeding attempts to replace themselves. Pairs in the Yellowstone study area would require 22 breeding attempts.

If the population declined but has reached a new equilibrium, analysis of the post-1968 cygnet production is more appropriate. The census data show that 400 cygnets were fledged in the last 4 censused years, an average of 1.1 cygnets fledged per active nest. At this level of productivity nesting pairs will replace themselves in about 8.8 years. Even at this rate the population will continue to decline.

Because of the delayed reproductive maturity of the Trumpeter, a time-lag will occur before the lack of recruitment reduces the number of breeding pairs in the Region. First, the age structure of both the breeding and non-breeding segments will shift downward as the 5- and 4-year-olds move into the breeding population. Then the size of the non-breeding segment will decrease as fewer cygnets survive their first 3 years of life. Changes in age structure will not be obvious but may be manifested in lowered mean clutch size, more pairs that nest without laying eggs, and poor parental care. The present slow decline in Regional adult numbers, without a corresponding decrease in the number of cygnets produced, may mean that the size of the non-breeding segment already is decreasing.

The current estimated summer population level of 405 adults was reached by 1951 and followed by a fluctuating but gradual increase for 13 years. That the same number of swans cannot presently sustain themselves in the same habitat suggests a decline in the Regional carrying capacity, similar to that noted at RRNWR, has already occurred.

Possible Causes of Cygnet Mortality

Coyotes, otter, and mink have been blamed for cygnet deaths in YNP (Condon 1941). Although some of the cygnets which disappeared without a trace in 1977 and 1978 may have been lost to predators, entire broods suffered a noticeable decline in vigor soon after hatching and died within a few weeks. Because of this weakness, their vulnerability to predators was high, but predation could not be considered the ultimate cause of their death. Dead cygnets and unhatched eggs lay for days, and sometimes weeks, untouched by predator or scavenger. Known predator kills were limited to two stunted cygnets and two incubating adults.

Past investigators suggested that the recent decline involves density-dependent factors acting on a population which reached, and probably surpassed, the carrying capacity of its breeding habitat in the 1950's (Banko 1960, Page 1976). Intraspecific stress and competition for limited breeding sites may be more apparent in the continuous marsh habitat of RRNWR where territory size, quality, and nearest neighbor distance may vary inversely with population size. Understanding how this competition would act to depress cygnet production in the discontinuous breeding habitat of the study area, where each pair is the sole occupant of a lake or pond, and separated by several km of forest from the next territory is more difficult.

One might reasonably hypothesize that, as the population increased, breeding pairs were forced to use less suitable lakes, and because of their lower success in these sites the average number of cygnets fledged at all active sites decreased. But this is not the case. Reconstruction of territory histories in YNP shows that most of the currently occupied territories were occupied by 1940 and those which currently fail to fledge young used to be much more productive. The seven territories which fledged 97 cygnets between 1931 and 1954, and only one cygnet since 1955 illustrate the magnitude of the change.

The presence of a few unoccupied territories in the study area, the failure of swans to nest at Harriman State Park in 1978 (R. Sandow personal communication), and the fluctuation in the number of breeding pairs at RRNWR between 34 and 60 in the last decade (R. Sjostrom personal communication) suggest that some factor other than breeding habitat limits population growth and expansion out of the immediate Tri-state area.

If habitat is a limiting factor, wintering, rather than breeding habitat, probably is in short supply. Small numbers of Trumpeters winter throughout the Tri-state Region wherever slow moving stretches of open water occur, but the 16 km of the Henry's Fork River near the village of Last Chance, Idaho, has held from 50 to 70% of the mid-continental population in recent years. Most of the remaining swans wintered at RRNWR where natural winter habitat is inadequate and where they depended on artificial feeding.

Important wintering sites were destroyed by the creation of the Island Park and Jackson Lake dams (Banko 1960). Increased winter recreational use and development along rivers has compressed the available winter range and further concentrated the swans within the isolation of Harriman State Park. Movements of swans into the center of the Park on weekends, when snowmobile use in bordering areas increases, may be an indication of the continuing problem.

Trumpeters can eat up to 9.1 kg (wet weight) of vegetation per day (Page 1976). An unmeasured amount is ripped out and washed downstream by the current as they loosen vegetation with their feet. Possibly, such a species historically employed a "rest-rotation" strategy of winter feeding, moving on to another site as the flock depleted the submergent vegetation in a particular location. Such a strategy is no longer possible unless the swans leave the Tri-state Region entirely. No other adequate, unused wintering habitat remains nearby for them to exploit.

Page (1976) found that increased winter feeding at RRNWR was followed the next summer by an increase in the number of nests, percent of eggs hatching, and cygnet survival. He hypothesized that reduced winter feeding caused the swans to enter the breeding season in poor condition and decreased their nesting success. I suggest that, under present conditions, most of the self-sufficient swans in the Region have a winter diet that satisfies maintenance requirements but leaves the breeding adults in marginal reproductive condition. If environmental conditions are mild during incubation and brood rearing, reproduction may be successful. However, harsh, or perhaps even typical, weather may exert greater energy demands than the nesting birds can successfully withstand.

From observations of captive nesting Trumpeters, Cooper (1978) found that the pre-laying period was a critical time during which the female fed intensively and built up energy reserves to sustain her through incubation. Incubation then followed a fasting strategy in which the female relied heavily on endogenous reserves and incubated quite independently of daily climatic fluctuations. Cooper observed an incubation constancy of 94.7% in 1975 and 95.7% in 1976 by the same nesting female. Mean recess time from four nestings involving two different females was 21 minutes (n = 32) with an average of four recesses per day in 1975, and three per day in 1976.

The photographed incubation behavior of six wild swans in the present study revealed constancies ranging from 78 to 89%. Each swan hatched at least one egg although constancies were lower at nests where total brood mortality later occurred. Recess length averaged 37 minutes (n = 384) and was longer at nests where all cygnets died. The small sample size certainly magnifies individual idiosyncrasies. But wild Trumpeters did not maintain the high constancy of incubation possible in captivity. The data also showed that certain swans lay small clutches, take frequent and long recesses, and suffer total brood mortality.

I hypothesize that reduced clutch size, increased time spent feeding, and poor cygnet viability result from depleted energy reserves of the incubating female. In extreme cases, the length of time spent off the nest may increase to the point where abnormal embryo development results from a slight decline in internal temperature (Drent 1973).

If the current winter habitat provides marginal food resources, the period between departure from the winter range and nest initiation becomes critical to increase the female's energy reserves. Trumpeters dispersed from the wintering grounds by early March. Local breeding residents soon moved to ice-locked territories, where they often sat on the ice for weeks. Opportunities to feed and restore depleted energy reserves prior to nesting thus were limited, particularly when spring thaw was delayed. Canadian Trumpeters, on the other hand, although facing a migration of some 1400 km, moved to lower elevations and milder climatic conditions where they increased their opportunity to feed during the pre-laying period. Greater clutch size and cygnet viability could result from such a feeding advantage.

The 57.1% mortality of Grande Prairie cygnets between fledging and age 1 (Turner and MacKay 1978) primarily occurs in late winter or during the spring migration, as most marked cygnets survived the fall migration to YNP and were intermittently observed on the Henry's Fork until March. If their winter diet were marginal, these newly fledged birds would be particularly vulnerable to the rigors of their first northward migration, as they seem to be.

Although the above evidence strongly suggests that winter habitat limitations exist, there is additional evidence that some of the current problems affecting the cygnets existed before the population reached a level where density dependent effects became significant. The pattern of general weakness, deformities, and slow growth, which predisposed the cygnets to death from predators, parasites, or harsh weather, was mentioned by several earlier observers.

Banko (1960) encountered a cygnet at RRNWR which possessed deformed feet while its broodmate was normal. He also quoted a 1946 report from Refuge manager W. Sharp:

> Three nests did not hatch and a fourth failed due to feet deformities of the cygnets. The latter nest, when checked on the Upper Lake, had three dead cygnets and another alive on the nest. Careful study revealed that the living cygnet could not stand. An examination of its feet showed that they were pitifully deformed. Then the dead cygnets were examined, and their feet were deformed in a similar manner.

A photograph taken by Sharp (Banko 1950) showed that the foot deformities were externally identical to those observed in cygnets from RRNWR and Cygnet Lake, YNP, in 1978.

Occasional retarded development also occurred in earlier years. Banko (1950) cited a 1949 report from the National Elk Refuge, Jackson, Wyoming, that "One of the cygnets raised this year is smaller than the other three and is still unable to fly (by December) due to an inadequate growth of wing feathers." In 1949, about 20 of the 61 cygnets reared at RRNWR were unable to fly by 15 October, even though most nests hatched by 25 June and the cygnets were at least 110 days old. One cygnet in particular possessed very poorly developed primaries (Banko 1950).

Certain breeding Trumpeters in the Tri-state Region seem chronically weakened and their broods suffer partial mortality, deformities, and slow growth during favorable environmental conditions.

During harsh spring weather, and/or when the birds are further stressed by competition, they suffer greatly reduced cygnet viability and the rapid loss of entire broods. Many unusual geologic features occur in the Yellowstone area, including known sites with "wild imbalances" of trace elements (D. Love personal communication). The gradual accumulation of a trace element such as selenium or radium is possible in a long-lived species such as the Trumpeter. Blood parasites would also be a likely endemic factor which could cause heavy mortality when the population is stressed.

The mountain climate is harsh and sometimes considered marginal (Johnsgaard 1978), but for over 20 years prior to 1954 the Regional population grew steadily in this habitat at an annual rate of about 10% (Banko 1960). Nesting in the Grand Teton National Park area was reestablished about the same time (Johnsgaard 1978) as the entire population began to experience a decline in productivity. The poor production in the Grande Teton vicinity since 1954 probably is linked to the overall population problems, rather than to habitat inadequacies.

Evidence does not indicate that the Tri-state habitat was marginal historically. Banko (1960), on the contrary, concluded that, although Trumpeters occurred over a broad geographic range, they were only common in three areas: the Flathead Valley of Montana, southern Minnesota and northern Iowa, and the Red Rock Lakes-YNP-Jackson Hole Region. Also, from about 1550 to 1900, the climate of the YNP Region was significantly colder as the Gannett Peak neoglacial stade or "Little Ice Age" caused later springs and earlier falls (Houston 1976). Yet as the Region emerged from this colder period, travelers mentioned the abundance of swan in the Region (Carpenter 1878, Banko 1960).

The historical occupation of the Tri-state Region and the rapid expansion of the population from about 1930 to 1954 proves that the Region does provide adequate habitat for the species. However, if the swans are weakened by competition, nutritional inadequacies, parasites, or disease, then the harsh environment may act to stress the nesting birds beyond the level of successful reproduction. This may often have been the case in recent nesting seasons.

Migrant Swans

Over 50% of the 200 Grande Prairie Trumpeters visited Yellowstone Lake. The breeding grounds of the remaining 200+ migrants is unknown. Since 1945, RRNWR personnel have tarsal-banded resident swans (Jonkel 1976), and well over 50% (64 of 80 captured on Lima Reservoir in July 1978) of the resident Trumpeters in the Region are banded. During this study, only two tarsal-banded Trumpeters were seen at Yellowstone Lake, and the lack of banded Trumpeters indicates that few Tri-state birds move to Yellowstone Lake. Many of the migrants may come from yet unidentified breeding grounds, possibly in the Yukon or Northwest Territories.

Significance of YNP

The establishment of YNP in 1872 played a major role in preventing the total extermination of Trumpeter Swans south of Alaska although this was not realized at the time. The presence of a breeding remnant in the area was not widely known until separate discoveries of nesting swans by Skinner and Smith in 1919 near Lewis and Delusion lakes, respectively (Skinner 1920).

Although roughly 15% of the adult population in the Region summers in Yellowstone, the Park's greatest significance is as a resting area during fall migration. A major cause of the Trumpeter's decline elsewhere was hunting of these conspicuous low flying birds, particularly when their migratory or wintering patterns led them into settled regions (Banko 1960). YNP preserved important habitat free from major hunting pressure during the October to December period. The early arrival of winter snows at Yellowstone Lake insured protection for the birds prior to official prohibition of hunting in 1883

(Haines 1977).

Specimens and statements from travelers in the late 1800's indicate that Trumpeters continuously occupied the YNP Region (refer to p. 4), even though they existed relatively unnoticed until Skinner aroused interest (Banko 1960). His discovery prompted further observations by Park personnel which showed that Yellowstone Lake has been an important swan migration stop for many years, although confusion existed regarding the specific identity of the migrants. Of 118 swans seen on Mary's Bay on 30 October 1930, 68 were closely examined and identified as Trumpeters. A month later, 300 swans of undetermined species were counted on Yellowstone Lake (Wright 1934). These counts compare favorably with existing levels of use.

The color-marking of Grande Prairie Trumpeters began in 1954 and a few birds were sighted in the Tri-state Region in 1955 and 1956 (MacKay 1957). The current neck-banding effort began in 1973 and swans from Alberta were sighted on the Yellowstone River in February 1974. Saskatchewan Trumpeters were found at RRNWR the same winter (YNP files).

The isolation and protection of YNP not only freed the remnant breeding population from human-caused mortality, but also was an important factor in preserving the relict migratory populations of Alberta and Saskatchewan. Swan families which traditionally migrated to this protected area escaped the slaughter suffered by those that migrated to more developed areas. Along with the extermination of the families which migrated to other more vulnerable wintering areas came the loss of their migratory traditions. Although population numbers have since increased, the lost traditions have not been restored.

Illegal shooting continues to be a mortality factor of marked Canadian Trumpeters (B. Turner personal communication), and the feeding habits of swans render them particularly vulnerable to lead poisoning caused by ingested lead shot. Results of the present study, showing that about one-half of the midcontinental population avoided these dangers of the waterfowl hunting season by gathering within YNP, reveals for the first time the importance of this area as an autumn refuge.

Although the current reproductive problems greatly reduce the number of cygnets produced in YNP, protection of this habitat will become more important in the future. As development and conflicting uses destroy the productivity of nesting sites on private and National Forest lands, the approximately 20 pairs which YNP can support will become a more important portion of the regional breeding population.

Mute Swans

The feral population of Mute Swans along the Yellowstone River south of Livingston, Montana, poses a grave potential threat to the Trumpeters. As they increase and continue to disperse further into Trumpeter habitat they will compete effectively for food and nesting sites. Their aggressiveness and greater tolerance of humans will give them an advantage over the more wary Trumpeters. Their mere presence near an active Trumpeter nest could evoke sufficient territorial defense to disrupt successful incubation. The Mute Swan has already demonstrated its reproductive potential in North America with the establishment of expanding populations in Michigan, Puget Sound, and the Chesapeake Bay area (Bellrose 1976). Reese (1975) discussed current competitive effects, vegetation destruction, and the need for wildlife managers to face the problem of Mute Swan expansion.

In addition to the threat of interspecific competition, there is a real possibility that hybridization with wild Trumpeters may occur. The pairing of a Trumpeter and a Mute at Harriman State Park in the winters of 1977-78 and 1978-79, illustrates the potential.

Winter Habitat Protection

Current management plans for Harriman State Park recognize the unique role that this area plays as the primary wintering site for the midcontinental population and strictly limits human disturbance within Park boundaries.

The flow of water through the Park, however, is controlled by the Island Park Dam, 10 km upstream. A reduction of flow during one of the occasional severe cold spells (-40°C and below) which occur almost every year could cause almost total freezing of the main wintering sites. Only the most rapid stretches of river would remain open, and these areas have little potential to support swans.

Trumpeters at Lonesome Lake, B.C. and RRNWR have shown a reluctance to leave a traditional winter feeding site even when faced with starvation. Swans remain and weaken to the point where flight becomes impossible. If the Henry's Fork wintering area freezes solidly, no alternate wintering site exists to which 400 to 500 swans could move unless they were strong enough and inclined to leave the region entirely. Some birds would move to RRNWR in search of grain, but the Canadian swans have shown little tendency to explore that area. A poorly timed reduction in flow at the Dam could easily create a crisis in the already difficult wintering situation, causing additional stress and possibly direct mortality.

<u>Concentration of Swans</u>

Regardless of the winter habitat quality, the security of the entire midcontinental population is threatened by its concentration within such a limited wintering area. The purpose of previous transplant efforts was to insure that no single catastrophe could wipe out the last known Trumpeter Swan population. The existence of Trumpeters in Alaska and the success of the LaCreek NWR transplant greatly lessen the probability of species extinction. The discovery that virtually every Trumpeter breeding south of Alaska migrates to the Tri-state Region and winters within a 100 km radius of Island Park, Idaho, however, reveals the continued vulnerability of this population. As long as the RRNWR Trumpeters congregate to receive grain and the majority of the off-Refuge swans winter together on the Henry's Fork, the chances for a catastrophe, such as infectious disease, to occur are great. If competition decreases the swans' energy reserves, their vulnerability to such an event will increase.

CHAPTER VI

MANAGEMENT RECOMMENDATIONS

Yellowstone National Park

1. Eliminate the parking areas along the road adjacent to "Beach Springs Lagoon" to reduce visitor access to the swan nest.
2. Close all campsites and fishing at Grebe Lake until 1 July or until cygnets have hatched. Several years of closures may be required before swans again resume nesting.
3. If Recommendations 1 and 2 do not suffice to correct the present situation within 3 years, a nesting island should be built in both territories. A small island, 1 x 2 m in size, situated in about 1 to 1.5 m of water and located at least 10 m from shore would give the swans a suitable nesting site, protected from human harassment. Although this is an artificial solution, it may be necessary to compensate for the current unsuitability of shoreline nesting sites resulting from human disturbance. The island should be planted with native vegetation so that adequate nesting materials will be available.
4. Obliterate the trail to Harlequin Lake. Day use and illegal camping were common at this territory. NPS personnel,

particularly those working in the Madison Junction campground, should not direct visitors to this Lake, particularly prior to 15 July.

5. No new campsites or trails should be built at historic nesting lakes. In particular, new campsites should not be placed on the shore of Riddle Lake south and west of the outlet. This area should be left undisturbed as a waterfowl sanctuary. Existing campsites on the north and east shores should remain closed until after the cygnets hatch, usually about 1 July but as late as 15 July during a late, cold spring.
6. Prohibit boating in the western arm of Shoshone Lake within 1 km of the outlet of Cold Mountain Creek, and close campsites in this same area until after 15 July.
7. Obliterate the present trail leading west from Trail Creek Cabin and reroute it away from the shore of "Trail Creek Pond." Do not, however, begin this project while the swan family remains on the Pond. Human disturbance after hatching may have caused this family to abandon the Pond both in 1977 and 1978 and contributed to the loss of both broods.
8. Destroy any Mute Swans or nests found in the Park, recording data on nesting site characteristics, clutch size, and egg fertility. Any evidence of nesting or hybridization involving Mute Swans should be relayed to the USFWS at RRNWR.

9. No future activities should be planned which would increase human use of the north shore of Yellowstone Lake and the Yellowstone River from Fishing Bridge to Alum Creek after 20 October. The outlet of Pelican Creek and the west side of Storm Point deserve particular attention.

10. Continue to locate all active nests, and monitor nesting attempts and cygnet production. Information on the cygnet production of each territory from 1931 to 1978 is available in the Resource Management Office files along with a map showing territory locations. This unique record should be continued through two annual aerial surveys. The first, a 6-hour flight about 15 May, should search all historic nesting territories, census all adults, and determine the status of breeding activity and location of active nests. Campsites at all backcountry lakes where an active nest exists should be closed until at least 1 July. Historic territories where swans fail to nest should be checked by the Resource Management Office to detect any increase in human activity at the site. The second flight will require about 5 hours in early September to census cygnet production. All territories should be checked to detect birds that initiated nesting after the first survey. The September survey should coordinate with the USFWS Tri-state Trumpeter Swan Survey when possible. Intensive monitoring should continue at least until population stability is apparent.

11. Participate with the USFWS in the mid-winter Trumpeter Swan Survey. Accurate censusing of wintering flocks provides the only available data on the trend of the entire population. Up to 100 Trumpeters may winter in Yellowstone although numbers usually are much lower.

<u>Regional</u>

1. To disperse the wintering swans and lessen their vulnerability to disease or habitat destruction, the USFWS should establish at least two additional wintering areas outside of the Tri-state Region. Preferably these would be refuges which could be managed to enhance winter swan food production.

   Methods should be developed and tested to teach new wintering traditions to migratory Trumpeters. Conceivably this could involve the capture of Canadian cygnets in late September prior to fledging. Family groups might be held at the chosen wintering site and released the following spring. An extensive review of the literature and adaptation of methods used on other waterfowl species will be necessary.
2. Water release at Island Park Dam should be coordinated to benefit wintering Trumpeters by lessening the chances of a major freezing of the Henry's Fork in the Island Park vicinity. The Bureau of Reclamation should consult with the USFWS personnel

at RRNWR and with the Idaho Department of Fish and Game biologists before making any interruptions in water flow through the wintering grounds. Allowing outflow over the Dam to equal inflow into the reservoir would roughly give the swans the water flow they would receive if the Dam did not exist. Active management to benefit Trumpeters could include the release of additional water during extreme cold periods to prevent freezing of the River. During the extreme cold weather of late December 1978 and early January 1979, water releases of between 366-404 cfs (Bureau of Reclamation files) sufficed to prevent freezing at Harriman State Park; this should serve as a guideline for future winter release schedules.

3. As previously recommended by Page (1976), the USFWS late summer Tri-state Trumpeter Swan Census should be held on an annual, rather than tri-annual schedule, to accurately assess the population trend and avoid the continuing loss of valuable data on production.

4. The USFWS mid-winter Trumpeter Swan Survey should routinely include at least 1 day of ground observations at Harriman State Park and along the Teton River near Victor and Driggs, Idaho (Lat. 43°43', Long. 111°10'), to determine the proportion of Whistling Swans included in the aerial count.

5. Sampling should be conducted bi-annually in early October to

provide baseline data on vegetation trends in the Henry's Fork River at Harriman State Park. Park personnel have identified the particular stretches of River that receive the most concentrated use, and research into the species composition, production, and trend of food plants is needed.

6. RRNWR should serve as a clearing-house of current information and technical expertise on Trumpeter Swans so that the various concerned agencies can obtain accurate population information. The numerous State and Federal jurisdictions have fragmented the understanding and management of the midcontinental population as a whole.

7. The establishment of a feral Mute Swan population in the Tri-state Region should be prevented. Destruction of all nests and birds, particularly those found in occupied Trumpeter habitat or paired with Trumpeters, is necessary. The core flock on the Yellowstone River should be eliminated before it increases and disperses further. Legislation to prevent the intentional release of this species in the Region may be necessary if existing state laws are inadequate.

8. Land management agencies should direct human activity away from wintering and nesting sites. Timber cutting practices that leave a visual barrier between a nesting lake and the nearest road or trail would minimize disturbance to swans. Winter activities

such as snowmobiling or cross-country skiing will cause most swans to fly if the person can be seen. Snowmobile and ski trails should be routed away from the river courses.

9. Swan nesting habitat could be improved by deepening ponds which currently dry up during the summer. Water depths of 1 to 2 m provide good feeding opportunities. The creation of a nesting island, if one is lacking, could increase the suitability of some territories, particularly where human use occurs.

10. Future research into the causes of the weakness, deformities, and high cygnet mortality must include the live capture of moribund cygnets. Detailed blood and tissue studies cannot be conducted on contaminated, partially decomposed specimens retrieved after death in the wild. Detailed necropsies on freshly dead cygnets have not been made to date.

CHAPTER VII

SUMMARY

The ecology of nesting and migrant Trumpeter Swans in Yellowstone National Park (YNP) and vicinity was studied from September 1976 to April 1979. The primary objectives were to: assess the current status of Trumpeters in the study area, identify the causes of low cygnet production, determine whether human activities reduce cygnet production in YNP, and follow the movements of neck-banded migrant Trumpeters.

The 6400 km^2 study area contained 30 nesting pairs of Trumpeters, roughly 33% of the breeding population of the entire Tri-state Region. The 21 pairs found nesting in YNP represent approximately a 50% increase compared to the previous high count of 13 breeding pairs in 1939 (Condon 1941).

During 1977 and 1978 combined, clutch sizes averaged 4.21 eggs at 33 nests and was significantly reduced to 3.80 eggs per nest in 1978. Cold weather and heavy snowpack delayed nest initiation in 1978 from 1 to 3 weeks at most territories.

The estimated hatching rate of eggs was 49%. Nesting success varied from 71% in 1977 to 41% in 1978. Losses to flooding during the

peak runoff in late May and the infertility of three complete clutches accounted for much of the 1977 decrease.

Six of the 48 nesting attempts were abnormal. In five cases the adults nested but failed to lay eggs; two pairs had this difficulty both in 1977 and 1978. The sixth case involved two females that paired, and each laid and incubated an infertile clutch of five eggs.

At six nests, the pattern of incubation was quantified via time-lapse photography. The three nests that fledged young contained larger clutches than the three nests that failed, and the successful females incubated with greater constancy, greater session length, shorter recesses, and fewer recesses per day than did their unsuccessful counterparts. These "better" incubators also had a higher hatching rate of eggs and higher cygnet survival. Multiple regression analysis showed that variation in the number of recesses per day and in session lengths accounted for 89.17% of the variability in the number of cygnets hatched, and 68.54% of the variability in the number of cygnets fledged.

Although incubation patterns were quantified at only six nests, the positive relationship between increased clutch size and increased cygnet survival was true throughout the study area. Cygnets from clutches of four or fewer eggs suffered 90% mortality, with a complete loss of 75% of the broods. Cygnets from clutches of five or six eggs suffered 69% mortality, with a loss of 42% of the broods. Clutch size normally is reduced among birds nesting for the first time, or when the female is in poor physical condition. At each territory, clutch size either remained the same or decreased from 1977 to 1978; a combination of the late spring and the females' poor condition were probably more important factors in this reduction than the females' ages.

Mean brood size at hatching was 1.8 cygnets per active nest. Of the 87 cygnets that hatched, 66 (76%) died prior to fledging. These deaths included the complete loss of 15 of the 26 broods. Virtually all mortality occurred within the first 6 weeks of life. Necropsies on nine cygnets could not determine the cause of death. Moribund cygnets showed overall weakness, leg and foot deformities, and rapid flicking of the head. Twenty-two percent of the cygnets that survived to September were retarded in development.

The hatching success of only 49% and the very high cygnet mortality prior to fledging were the major causes of the virtual lack of cygnet production in the YNP vicinity.

Human activity in YNP was the most important obstacle to successful nesting at Shoshone and Grebe lakes, and greatly reduced the chances of successful nesting at "Beach Spring Lagoon." Each territory lacked a suitable nesting island and the historic nesting site was on the shoreline where it now is extremely vulnerable to vandalism or unintentional disruption by humans.

Cygnet production did not vary significantly between disturbed and undisturbed territories. However, swans were more likely to be present at disturbed territories without nesting, or to be absent entirely, than they were at undisturbed territories. The number of nests established per territory, per year, was 0.91 at undisturbed territories and 0.69 at disturbed. Thus, the effects of disturbance are subtle. The swans that can habituate to human disturbance will suffer no reduction in nesting success (unless vandalism or a similar extreme event occurs), but disturbed territories will support fewer nesting attempts.

Between 300 and 450 migrant Trumpeters visited the Yellowstone Lake area from October to December. Most of these swans came from outside the Tri-state Region and represented most of the known Canadian breeding population. At least 69 different neck-banded Trumpeters from Grande Prairie, Alberta, passed through the area during the study.

As Yellowstone Lake froze, the swans moved south and west to join other migrants and year-round residents on the Henry's Fork of the Snake River, in and near Harriman State Park. Although a few scattered swans wintered throughout the Tri-state Region wherever slow moving, ice-free water existed, Harriman State Park provided winter habitat of unparalleled importance. Between 500 and 600 Trumpeters congregated in the Park during the coldest periods when most other areas froze. Most of the Canadian migrants used this site; less than a dozen neck-banded Trumpeters were detected wintering at Red Rock Lakes NWR.

The winter concentration of up to 68% of the midcontinental Trumpeters on less than 16 km of river presents a situation with high potential for either habitat depletion or the rapid spread of disease. Dispersal of wintering swans is necessary to provide a reasonable degree of security.

The water flow through Harriman State Park is controlled at the Island Park Dam. Manipulation of water releases to prevent freezing of the wintering site could be a valuable management tool to benefit the wintering swans.

In excess of 50 feral Mute Swans presently inhabit the Tri-state Region. Their continued increase and range expansion raises the threat of competition and possibly hybridization with the native Trumpeters. A Mute Swan, paired with a Trumpeter, was seen on two occasions.

At the current rate of reproduction (0.44 cygnets fledged per active nest), swans in the study area require 22 years to replace the pair unit. Region-wide production since 1968 equaled an estimated 1.1 cygnets fledged per active nest, a rate which will require 8.8 years to replace the pair unit.

Between 1964 and 1968, the Regional adult population decreased by 22%. In the last decade the decline has slowed and approached an apparent equilibrium of between 405 and 445 adults, but this leveling off probably is temporary. From the best available census figures and estimated age-specific survival rates, the population is not reproducing adequately to replace itself.

Both mortality data from the Canadian neck-banding studies, and the positive relationship between low clutch size, lowered attentiveness during incubation, and reduced cygnet viability found in this study point to poor physical condition of swans as they leave the wintering areas. Winter competition for limited food resources is a likely cause of the present problems.

Because of the greater stresses placed upon nesting birds by the rigorous, high elevation environment of YNP, factors that affect the reproductive success of swans throughout the Region may be felt most acutely in the Park. The current lack of successful reproduction in the study area seems to reflect a Regional density-dependent phenomenon that is causing infertility, small clutches, low hatchability, and high cygnet mortality. Further research is needed to determine the mechanisms involved. Concern is warranted because of the population's current inability to replace itself.

REFERENCES CITED

Banko, W. E. 1950. A contribution towards the life history of the Trumpeter Swan with notes on its status and management in the United States. Red Rock Lakes National Wildlife Refuge. 84pp. Mimeo.

________. 1960. The Trumpeter Swan. U.S. Dept. Int., N. Amer. Fauna 63. 214pp.

Barrows, M. 1936. Trumpeter Swans of Yellowstone National Park, summer 1936. U.S. Natl. Pk. Serv. Rept. 7pp. Mimeo.

________. 1937. Trumpeter Swan observations, summer 1939, Yellowstone National Park. U.S. Natl. Pk. Serv. Rept. 7pp. Mimeo.

Bellrose, F. C. 1976. Ducks, geese, and swans of North America. Stackpole Books, Harrisburg. 543pp.

Carpenter, F. 1878. The wonders of geyserland. In: Guie, H. D., and L. V. McWhorter, 1935. Adventures in geyserland. Caxton Printers, Caldwell, ID. 319pp.

Childs, F. W. 1934. Trumpeter Swans of Yellowstone National Park and adjacent vicinity, 1934. U.S. Natl. Pk. Serv. Rept. 7pp. Mimeo.

Coale, H. K. 1915. The present status of the Trumpeter Swan. Auk 32:82-90.

Condon, D. D. 1941. Preliminary report on the Trumpeter Swan of Yellowstone National Park. U.S. Natl. Pk. Serv. Rept. 27pp. Mimeo.

Cooper, J. A. 1978. Trumpeter Swan nesting behavior. J. Paper 10,358 of the MN Agri. Exp. Sta., Project 90. 32pp. Mimeo.

Delacour, J. 1954. Waterfowl of the world. Vol. 1. Country Life Ltd., London. 284pp.

Drent, R. H. 1973. The natural history of incubation. Pp. 262-311 in Farner, D. S. (ed.) Symposium on breeding behavior and reproductive physiology in birds. Natl. Acad. of Sci.

Farnes, P. E. 1973. Preliminary analysis of mean annual precipitation for Yellowstone National Park. Unpub. map, SCS, Bozeman, MT.

Hague, A. 1889. Notebook #1. 3894-1-1. Unpub. Nat. Archives. 93pp.

Haines, A. L., ed. 1965. The valley of the upper Yellowstone, an exploration of the headwaters of the Yellowstone River in the year 1869. U. of OK Press, Norman. 70pp.

________. 1977. The Yellowstone story, volume one. Yellowstone Library and Mus. Assoc. and the CO Assoc. U. Press, Boulder. 385pp.

Halladay, D. R. 1970. The historical distribution of the Trumpeter Swan in Canada. Trumpeter Swan Soc. News. No. 4. pp. 6-8. Mimeo.

Hansen, C. G. 1959. Report on the aquatic plants found in the Island Park area of Idaho during the fall and winter of 1958. USFWS Rept., Red Rock Lakes NWR, MT. 3pp. Mimeo.

Hansen, H. A., P. Shepherd, J. King, and W. Troyer. 1971. The Trumpeter Swan in Alaska. Wildl. Mono. No. 26. 83pp.

Holton, G. 1978. Trumpeter Swans in the Grande Prairie region of Alberta. U. of Alberta, Calgary. Prog. Rept. 4pp. Mimeo.

Houston, D. B. 1971. Ecosystems of national parks. Sci. 172:648-651.

________. 1976. The northern Yellowstone elk, parts III and IV, vegetation and habitat relations. U.S. Natl. Pk. Serv. Rept. Yellowstone Natl. Pk. 444pp. Mimeo.

Johnsgaard, P. A. 1973. Proximate and ultimate determinants of clutch size in Anatidae. Wildfowl 24:144-149.

________. 1978. The triumphant Trumpeter. Nat. Hist. 87(9):72-77.

Jonkel, G. M. 1976. A new aluminum Trumpeter Swan band. USFWS Rept., Laurel, MD. 5pp. Mimeo.

Keefer, W. R. 1972. Geologic story of Yellowstone National Park. Geol. Survey Bull. 1347. U.S. Govt. Printing Office, Washington, D.C. 92pp.

Leach, J. T. 1977. LaCreek area Trumpeter Swan behavior and migration study. Unpub. M.S. Thesis, U. of SD, Vermillion. 50pp.

Lensink, C. J. 1973. Population structure and productivity of Whistling Swans on the Yukon Delta, Alaska. Wildfowl 24:21-25.

MacKay, R. H. 1957. Movements of Trumpeter Swans shown by band returns and observations. Condor 59(5):339.

Martner, B. E. 1977. Climatological studies of Yellowstone and Grand Teton National Parks. U. of WY, Laramie. 198pp.

Morris, W. A. 1970. A brief on the status of the Trumpeter Swan (Olor buccinator) in British Columbia, 1969. Trumpeter Swan Soc. Newsletter No. 3. pp. 4-10.

Oberhansley, F., and M. Barrows. 1939. Yellowstone National Park Trumpeter Swan studies, 1938. U.S. Natl. Pk. Serv. Rept. Yellowstone Natl. Pk. 21pp. Mimeo.

Page, R. D. 1976. The ecology of the Trumpeter Swan on Red Rock Lakes National Wildlife Refuge, Montana. Ph.D. Dissertation, U. of MT, Missoula. 143pp.

Papike, R. 1970. Red Rock Lakes Trumpeters. Trumpeter Swan Soc. Newsletter No. 4. p. 2. Mimeo.

Paullin, D. G. 1973. The ecology of submerged aquatic macrophytes of Red Rock Lakes National Wildlife Refuge, Montana. M.S. Thesis, U. of MT, Missoula. 171pp.

Reese, J. G. 1975. Productivity and management of feral Mute Swans in Chesapeake Bay. J. Wildl. Manage. 39(2):280-286.

Rogers, P. M., and D. A. Hammer. 1978. Ancestral breeding and wintering ranges of Trumpeter Swan (Cygnus buccinator) in the eastern United States. Draft ms. Tennessee Valley Authority. 45pp.

Scharff, J. C. 1971. Malheur National Wildlife Refuge, Burns, Oregon. Trumpeter Swan Soc. Newsletter No. 5:6. Mimeo.

Scott, P., and the Wildfowl Trust. 1972. The swans. Houghton Mifflin Co., Boston. 242pp.

Sjostrom, R. 1978. Summary of the Trumpeter Swan mortality study 1962-66. Memorandum, Red Rock Lakes Natl. Wildl. Ref. 2pp. Mimeo.

Skinner, M. P. 1920. Trumpeter Swan breeding in Yellowstone National Park. Condor 22(2):72.

________. 1925. The birds of Yellowstone National Park. Roosevelt Wild Life Bull. NY State Coll. of Forestry, Syracuse. 3(1):153-157.

Skutch, A. F. 1962. The constancy of incubation. Wilson Bull. 74(2):115-152.

Trumpeter Swan Society. 1969. Newsletter No. 2:6. Maple Plain, MN. Mimeo.

________. 1971. Newsletter No. 5:13. Maple Plain, MN. Mimeo.

________. 1976. Newsletter No. 10:8. Maple Plain, MN. Mimeo.

Turner, B., and R. MacKay. 1978. The Trumpeter Swan population of Grande Prairie, Alberta. CWS Rept., Edmonton. 18pp. Mimeo.

U.S. Geologic Survey. 1972. Geologic map of Yellowstone National Park. Map I-711.

Vivion, O. 1969. Red Rock Lakes report. Trumpeter Swan Soc. Newsletter No. 1. p. 4. Mimeo.

Whitmore, S. B. 1974. Swans of the world. Taplinger Pub. Co., Inc., New York. 229pp.

Wingate, G. W. 1886. Through the Yellowstone Park on horseback. Judd and Judd, New York. 250pp.

Wright, G. M. 1934. Letter to the Director, National Park Service. Yellowstone Natl. Pk. files. 7pp. Mimeo.

________, J. S. Dixon, and B. H. Thompson. 1932. Fauna of the national parks of the United States. Wild Life Survey, Fauna Series No. 1. U.S. Govt. Printing Office, Washington, D.C. 157pp.

APPENDIX A

HISTORY OF SITE USE IN YNP, 1931 TO 1978; SITE USE IN THE GALLATIN AND TARGHEE NATIONAL FORESTS, 1977 AND 1978

History of Site Use in YNP, 1931 to 1978

Location	No. years swans present	Last successful brood	Total broods	Total cygnets	1977			1978		
					Swans	Nest	Cygnets	Swans	Nest	Cygnets
1. Riddle Lake	36	1978	21	48	yes	yes	1	yes	yes	1
2. East Tern Lake	34	1974	16	37	yes	yes	0	yes	yes	0
3. Swan Lake	27	1975	9	18	yes	no	0	yes	yes	0
4. Trumpeter Lake	27	1968	12	43	yes	yes	0	yes	yes	0
5. White Lake	27	1963	4	6	yes	yes	0	yes	yes	0
6. Shoshone Lake	26	1962	6	14	yes	no	0	no	no	0
7. Harlequin Lake	25	1955	11	33	yes	yes	0	yes	no	0
8. Fern Lake	24	...	0	0	no	no	0	no	no	0
9. Geode Lake	24	1963	10	33	no	no	0	no	no	0
10. Heart Lake	24	1961	4	14	no	no	0	no	no	0
11. Ponds south of Delusion Lake	22	1965	7	10	yes	yes	0	yes	yes	0
12. "Beach Spring Lagoon"	21	1974	9	23	yes	no	0	yes	yes	0
13. Grebe Lake	21	1952	10	24	yes	no	0	yes	no	0
14. Lilypad Lake	20	1960	1	2	no	no	0	no	no	0
15. Cygnet Lake	15	1952	3	5	yes	yes	0	yes	yes	0
16. Robinson Lake	15	1965	6	17	no	no	0	no	no	0
17. Grizzly Lake	14	...	0	0	no	no	0	no	no	0
18. Wolf Lake	13	...	0	0	no	no	0	no	no	0
19. Delusion Lake	12	...	0	0	no	no	0	no	no	0
20. Mouth of Slough Creek	12	1974	2	6	no	no	0	no	no	0
21. Madison River	12	1978	4	8	yes	yes	3	2 pr.	2	1
22. Bridger Lake	11	?	?	?	no	no	0	no	no	0
23. Trail Lake	11	...	0	0	no	no	0	no	no	0
24. Beula Lake	10	...	0	0	no	no	0	no	no	0
25. "Little Robinson Pond"	10	1955	5	16	yes	yes	0	yes	yes	0
26. "Phone Line Lake"	9	1958	3	11	no	no	0	no	no	0
27. Cascade Lake	8	...	0	0	yes	no	0	yes	no	0
28. "Calf Creek Pond"	8	...	0	0	yes	yes	0	yes	yes	0
29. Yellowstone Delta	9	1977	3	3	yes	yes	1	2 pr.	2	0
30. Obsidian Lake	7	1949	1	2	no	no	0	no	no	0
31. "Bunsen Peak Pond"	7	...	0	0	yes	yes	0	no	no	0
32. "Foster Lake"	6	1974	1	3	yes	no	0	yes	yes	0
33. Lewis Lake	4	1936	2	3	no	no	0	no	no	0
34. Winegar Lake	4	1937	1	3	no	no	0	no	no	0
35. "Geode Pond"	?	1977	?	?	yes	yes	2	no	no	0
36. "Richards Creek Pond"	?	...	0	0	yes	yes	0	yes	yes	0
37. "Trail Creek Pond"	?	...	?	?	yes	yes	0	yes	yes	0

Site Use in the Gallatin and Targhee National Forests, 1977 and 1978

Location	No. years swans present	Last successful brood	Total broods	Total cygnets	1977			1978		
					Swans	Nest	Cygnets	Swans	Nest	Cygnets
1. Aldridge Lake	unknown	1977	2	5	yes	yes	2	yes	yes	0
2. Rock Lake	unknown	...	unknown	unknown	yes	yes	0	yes	yes	0
3. Widgit Lake	unknown	1977	unknown	unknown	yes	yes	1	yes	yes	0
4. Indian Lake	unknown	...	unknown	unknown	yes	yes	0	yes	yes	0
5. Thompson Hole	unknown	1978	unknown	unknown	yes	yes	3	yes	yes	3
6. Winegar Hole	unknown	...	unknown	unknown	no	no	0	yes	yes	0
7. Ernest Lake	unknown	...	unknown	unknown	unknown	unknown	unknown	yes	yes	0
8. "Long Meadow Pond"	unknown	...	unknown	unknown	unknown	unknown	unknown	yes	yes	0
9. Chain Lake	unknown	1978	unknown	unknown	unknown	unknown	unknown	yes	yes	4

APPENDIX B

EGG MEASUREMENTS

Clutch	Maximum width		Maximum length
1.	75.8	x	110.7
	75.3	x	112.4
	75.5	x	112.8
2.	74.2	x	118.9
3.	74.6	x	118.9
4.	72.8	x	115.1
	72.5	x	109.6
	72.8	x	110.1
	74.6	x	108.8
	72.2	x	114.0
5.	68.6	x	108.0
	72.2	x	114.8
	76.9	x	115.1
	73.0	x	112.3
	75.5	x	113.7
6.	74.0	x	115.6
7.	75.6	x	113.1
	75.9	x	112.7
	72.4	x	111.6
	75.8	x	113.4
	75.6	x	114.6
	75.8	x	111.9
8.	69.8	x	107.5*
	68.6*	x	113.7
9.	72.8	x	110.0
	73.0	x	112.2
10.	71.6	x	114.0
	73.8	x	114.9
	72.8	x	113.5
	72.8	x	113.3
	73.1	x	112.3
11.	73.0	x	112.7
12.	73.7	x	122.9
	75.6	x	117.4
	74.1	x	121.9
13.	70.8	x	115.0
	71.2	x	116.0
14.	74.9	x	115.7
	75.6	x	112.6
	75.0	x	111.4
15.	71.9	x	114.5
16.	76.9*	x	117.0
	76.8	x	123.5*
17.	73.5	x	116.3
	75.9	x	122.2
	$\overline{w}$ = 73.75	x	$\overline{l}$ = 114.19
	S.D.= 2.05		S.D.= 3.66

*Extreme values.

APPENDIX C

COMPARISON OF TRUMPETER PRODUCTIVITY IN VARIOUS LOCALES

	Year	No. active nests	% successful nests	Mean clutch size	% eggs hatched	Cygnets hatched / active nest	Cygnets hatched / successful nest	% pre-fledging mortality	Cygnets fledged / active nest	Cygnets fledged / successful nest
YNP study area (this study)	1977-78	48	54	4.2	49	1.8	3.3	76	.44	.81
RRNWR (Refuge files)	1978 1976 1975	118	72	4.2	56	2.3	3.2	58	.97	1.3
(Page 1976)	1971-73	127	76	4.85	55.5	2.6	3.35	72.8	.71	.94
LaCreek NWR, South Dakota (Leach 1977)	1963-76	60	...	6.2	65	4.0	...	42	2.3	...
Grande Prairie (Holton 1978)	1978	14	93	5.6	73	4.3	4.6	55	1.9	2.1
Copper R., Alaska (Hansen et al. 1971)	1958 1959 1968	53	76	4.9	55	...	...	15-20	...	...

APPENDIX D

TRI-STATE SUMMER SURVEYS
(adults-cygnets)

	Idaho	RRNWR	Other Montana	YNP	GTNP	Elk Ref.	Other Wyoming	Total
1978	*	*-35	*	50-2	*	*	*	*
1977	60-7	137-39	132-28	51-10	14-6	4-0	7-5	405-95 (500)
1976	*	*-45	*	52-1	*	*	*	*
1975	*	*-34	*	*	*	*	*	*
1974	71-17	125-33	157-16	52-7	30-10	4-0	6-0	445-83 (528)
1973	*	*-39	*	*	*	*	*	*
1972	*	*-20	*	*	*	*	*	*
1971	60-6	146-12	151-37	30-3	27-10	2-0	15-0	431-68 (499)
1970	*	*-50	*	*	*	*	*	*
1969	*	*-15	*	*	*	*	*	*
1968	88-6	155-90	87-33	57-4	29-14	3-2	12-5	431-154 (585)
1967	85-8	184-20	120-5	55-2	24-5	6-3	14-2	488-45 (533)
1966	62-21	240-65	111-12	57-12	26-4	7-4	11-8	514-126 (640)
1965	64-12	190-16	164-20	60-5	24-0	10-2	27-6	539-61 (600)
1964	46-7	180-22	222-9	61-8	26-1	4-0	15-1	554-48 (602)
1963	63-32	148-127	84-16	49-7	23-4	5-0	12-1	384-187 (571)
1962	45-18	179-53	46-33	44-7	13-0	13-0	26-2	366-113 (479)
1961	47-19	155-14	100-15	71-3	21-8	23-0	13-1	430-60 (490)
1960	95-23	163-34	131-16	56-7	36-6	2-0	0-0	483-86 (569)
1959	44-10	271-40	108-19	62-8	26-8	5-5	16-9	532-99 (631)
1958	59-38	270-40	92-24	64-18	17-9	3-0	21-18	526-147 (673)
1957	27-4	159-45	88-12	44-16	13-6	2-0	26-6	359-89 (448)
1956	26-14	293-39	81-9	48-9	10-6	6-0	17-4	481-81 (562)
1955	40	242-41	132	58-10	10-5	14	25-10	(587)

APPENDIX D (continued)

	Idaho	RRNWR	Other Montana	YNP	GTNP	Elk Ref.	Other Wyoming	Total
1954	38-7	352-28	60-12	64-23	8-4	10-3	16-2	548-79 (627)
1953	61-30@	211-38	142-19	51-10	2-4	5-2	*	470-99 (569)
1952	60-10	184-55	156-12	58-3	0	5-3	5-3	468-86 (554)
1951	46-18	170-76	115-13	63-11	*	6-0	*	400-118 (518)
1950	31-7	106-40	81-7	57-16	*	4-3	*	279-73 (352)
1949	29-7	132-61	101-14	54-21	*	5-0	*	321-103 (424)
1948	34-4	121-73	78-12	49-13	*	6-4	*	288-106 (394)
1947	24-0	131-49	48-3	54-8	*	6-0	*	263-60 (323)
1946	23-0	124-46	57-16	47-10	*	4-0	*	255-72 (327)
1945	16-0	113-50	35-2	*	*	*	*	168-52 (220)
1944	22-0	106-58	31-3	35-8	*	4-3	13-3	211-75 (286)
1943	8-0	88-25	41-9	*	*	3-0	*	140-34 (174)
1942	24-0	45-43	26-10	*	*	3-0	*	98-53 (151)
1941	19-0	52-44	18-10	44-15	*	3-0	*	136-69 (205)
1940	7-5	58-48	9-1	43-14	*	3-0	*	120-68 (188)
1939	12-0	50-59	8-0	*	*	*	*	70-59 (129)
1938	*	26-42	23-9	40-4	*	*	7-0	96-55 (151)
1937	3-0	34-51	2-0	40-28	*	*	6-3	85-82 (167)
1936	3-2	31-26	*	38-12	*	*	2-0	74-40 (114)
1935	*	30-16	*	16-11	*	*	*	46-17 (63)
1934	13-5	16-26	*	16-17	1-0	*	2-1	48-49 (97)
1933	4-0	15-9	2-0	27-8	1-0	*	*	49-17 (66)
1932	7-0	19-7	1-2	29-2	2-1	*	*	58-12 (70)
1931	*	*	*	14-12	6-3	*	*	20-15 (35)

* = area not surveyed.

@ = Idaho and Wyoming combined.

APPENDIX E

MID-WINTER SURVEYS, U.S. FISH AND WILDLIFE SERVICE

	Idaho	RRNWR	Other Montana	YNP	GTNP	Elk Ref.	Other Wyoming	Total
1979	353-81	253-20	51-6	71-13	6-0	3-0	6-3	743-123 (866)
1978	392-96	141-48	53-20	46-11	4-4	12-0	47-0	695-179 (874)
1977	395-126	290-34	25-9	43-9	14-0	24	48-0	839-178 (1017)
1976	308-67	203-18	50-16	32	8-1	17-0	5-0	623-102 (725)
1975	333-94	151-28	41-4	30	26-2	14-0	*	595-128 (723)
1974	282-109	229-37	4-3	31-7	2-0	5-0	*	553-156 (709)
1973	226-58	212-28	*	61	*	*		434-86 (585)
1972	154-14 149-0	145-11	64-3	56	16-4	*	*	584-32 (616)

* = area not surveyed.

APPENDIX F

IDAHO DEPARTMENT OF FISH AND GAME
WINTER SWAN COUNTS

Island Park, Idaho
(Harriman State Park vicinity)

Year	Count
78-79	598
77-78	598
76-77	439
75-76	496
74-75	519
73-74	314
72-73	549
71-72	325
70-71	71
69-70	192
68-69	261
67-68	367
66-67	285
65-66	201
64-65	282
63-64	169
62-63	128
61-62	384
60-61	161
59-60	387
58-59	246
57-58	230
56-57	323
55-56	...
54-55	271
53-54	378