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Factors Influencing the Distribution, Abundance, and Reproductive Success of Ospreys in Voyageurs National Park, Minnesota



United States Department of the Interior

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FACTORS INFLUENCING THE DISTRIBUTION, ABUNDANCE, AND REPRODUCTIVE
SUCCESS OF OSPREYS IN VOYAGEURS NATIONAL PARK, MINNESOTA

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ABSTRACT

Ospreys (Pandion haliaetus) were studied for two breeding seasons in Voyageurs National Park, Minnesota, to determine factors that influence their distribution, abundance and reproductive success. Osprey distribution and reproductive success was estimated from aerial and ground nest surveys conducted in spring and late summer. Nests were categorized according to their proximity to the four largest bodies of water which represented different levels of water fluctuation, fish productivity and human disturbance. The population in Voyageurs National Park consisted of 24 pairs of nesting birds in 1985 and 1986; the distribution of nest sites was clumped during each of these seasons. One group of nests was located in several bays off Grassy Bay in Sand Point Lake, a second was on the south shore of Kabetogama Lake and a third was located on the west end of Kabetogama Lake adjacent to Black Bay on west Rainy Lake.

Water level fluctuations differ in two regions of the Park. The average annual water level fluctuation in Rainy Lake is 1.0 m while in the Namakan Reservoir it is 2.7 m. The patterns of these fluctuations vary from those of natural fluctuations and simulate flood and drought conditions. Lake productivity was measured as relative abundance of fishes, determined by catch per unit effort in experimental gill nets. These data indicated that Kabetogama Lake was the most productive followed by Rainy, Sand Point, and Namakan lakes. Human disturbances were infrequent; when they occurred Osprey responses were minimal consisting either of no response or looking at the source of disturbance. However, disturbance within 50-100 m of the nest elicited alarm and defense behavior from the adult birds.

Mean reproductive success for 1985 and 1986 was 1.04 fledglings per occupied nest; it did not differ significantly among regions. Reproductive and fledging success data of Voyageurs Ospreys are intermediate between those reported in other studies and population growth appears to be stable.

There is no evidence that Osprey abundance, distribution and reproductive success are influenced directly by differences in water level fluctuation, lake productivity or human disturbance among regions. However, because water level fluctuations may suppress populations of fish species that are important components of Osprey diet, water levels may indirectly influence nest site distribution and foraging behavior. Whether or not water levels affect reproductive success, and ultimately Osprey population dynamics in Voyageurs National Park, is difficult to determine. Ospreys appear to compensate for regional differences in availability of fish by traveling the distance needed to secure food for their offspring. In a food stressed population regional differences in reproductive success might be more pronounced. The most important factors that currently appear to be influencing Osprey numbers in the Park are: (1) a large beaver population that creates new nest trees through pond construction, (2) large and diverse populations of fish throughout the Park, and (3) minimal human disturbance.

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INTRODUCTION

Voyageurs National Park is the only mainland U.S. national park located in a southern boreal forest region. About two thirds of the park is land and the remainder is numerous large and small lakes. Almost a century ago, Minnesota representatives recognized the uniqueness of this as yet unsettled wilderness on the boundary between Canada and the United States and requested that it be established as a national park. This effort failed and a long period of exploitation and development followed. Voyageurs was eventually established as a national park in 1975, but years of human activity had significantly altered many aspects of the original natural conditions; these included changes in lake levels, and in distribution, diversity and abundance of plant and wildlife populations.

One of the biggest challenges in management of the Park has been to determine what historical conditions were in the area before European settlement, and to recommend actions to restore or preserve representative examples of the natural southern boreal forest environment (Cole 1982 a,b). The purpose of this study was to identify factors that influence the current distribution, abundance, and reproductive success of the Osprey (Pandion haliaetus) in Voyageurs, and to compare present conditions and population status with reconstructions of the probable environment and population characteristics that existed before lake levels were manipulated by humans.

The Osprey is a large, fish-eating raptor found throughout temperate and tropical regions of the world (AOU 1983). Ospreys always nest on or adjacent to water, and feed almost exclusively on fish; thus Osprey population characteristics are influenced by changes in the aquatic environment. These natural history traits make the Osprey an important species for study in Voyageurs. During this study we attempted to answer the following questions: (1) What is the present distribution and abundance of Ospreys in Voyageurs? (2) What is the measure of water level fluctuation, lake productivity, and human disturbance in the region where each nest site is located? (3) How does human activity influence the behavior of Ospreys? (4) Is there a difference in foraging behavior among Osprey pairs using different nest sites? (5) What is the reproductive success (fledglings/pair) of Ospreys in Voyageurs? (6) Is the pattern of distribution and reproductive success influenced by variations in water levels, fish productivity, and human disturbance? (7) How do present distribution, abundance and reproductive success compare to that recorded in previous seasons? (8) How do present population characteristics of the Voyageurs Osprey population compare with other similar populations and with probable reconstructions of possible natural densities in the Park during presettlement times? (9) What future trends can be expected in the Voyageurs Osprey population?

METHODS

Study Area

Voyageurs National Park encompasses approximately 891 km², of which 61% is land and 39% is water. The Park is 62 km from east to west and ranges from 3 to 22 km from north to south. The northern boundary follows the U.S./Canadian border for about 80 km. Four major lakes lie partially within the park and account for 96% of the Park's water area.

Water levels in the four major lakes are regulated by a dam at the outlet of Rainy Lake and by two smaller dams located at the outlet of Namakan Lake. These dams control the levels of Kabetogama, Namakan and Sand Point lakes. Operation of the dams and the lake levels are controlled by general regulations established by the International Joint Commission. The operating plan is commonly referred to as the "rule curve"; it defines the maximum and minimum levels the water can reach at any given time.

Under the present "rule curve" the average annual water level fluctuation in Rainy Lake is 1.0 m while in Namakan Reservoir (includes Kabetogama, Namakan, and Sand Point Lakes), it is about 2.7 m. The U.S. Army Corps of Engineers projected that water level fluctuation in these lakes would be approximately 1.9 m without regulation (Flug 1986). In addition, the natural fluctuations differ from regulated fluctuations by: (1) usually reaching a peak in late May or early June instead of late June or early July; (2) tending to decline rather than remain stable over summer and fall; and (3) declining about 0.6 m instead of 1.8 m (in lakes with 2.7 m fluctuations) over winter. These patterns differ from a natural cycle in that they tend to simulate flood and drought conditions on an annual cycle (Kallemeyn 1985; Flug 1986).

General Observation Methods

Osprey nests were found by aerial survey and their locations plotted on topographical maps. They were categorized according to their proximity to the four largest bodies of water in the Park: Kabetogama Lake (Kabetogama), Rainy Lake (Rainy), Namakan Lake (Namakan), and Sand Point Lake (Sand Point). Namakan Lake and Sand Point Lake are treated as one region in this report and are referred to as Namakan/Sand Point (Namakan/Sand Point). Regions were chosen on the basis of Park records which indicated varying levels of water level fluctuations, fish productivity, and human disturbance.

Using a Planix 5 Tamaya Digital Planimeter, we determined that the land areas of each region were approximately the same size. The Kabetogama region covered 177 km², the Rainy Lake region 151 km², and the Namakan/Sand Point region 193 km². Regions are included in all map figures in this report.

Nests were assigned the same variables given the lake on which they were located. Selection of nests for intensive monitoring was based on the ability of assistants to observe the habitat around the nest, and on ease of access to each nest. Nests were visited on a rotating basis during both

summers. In 1985, we observed the following nests on a weekly basis: (1) Kabetogama Lake: Blind Ash Beaver Pond, Wood Duck Island (for human disturbance only), West LaBonty's Pond, Mud Bay Pond II, and North Deer Creek; (2) Rainy Lake: Hitchcock Pond, Cranberry White Rock Pond, Dove Bay-E, and Kempton Pond II; (3) Namakan/Sand Point Lakes: Staeger Bay Pond, Brown's Bay-West, and South Grassy Pond II. In 1986, we observed the following nest sites on a biweekly basis: (1) Kabetogama Lake: Blind Ash Beaver Pond, Wood Duck Island, West LaBonty's Pond, and Mud Bay II; (2) Rainy Lake: Cranberry White Rock Pond, and Dove Bay-E; (3) Namakan/Sand Point Lakes: O'Leary Lake Pond, and Brown's Bay-West. National Park Service code numbers for these nests are included in Figure 1. Nests were observed using a 7 x 35 binocular and a 15-60x spotting scope.

Osprey Biology

Census Methods.--To determine Osprey distribution and estimate number of nesting pairs, an aerial census of all known nests within and on the periphery of Voyageurs National Park was conducted in 1985 and in 1986. This census was timed to correspond with the incubation period (Dunstan 1973); the 1985 census was made in mid-June, and the 1986 census was conducted in early May. Nests were designated occupied (one or two adult Ospreys present) or unoccupied (no Ospreys present) according to standard reproductive terminology outlined by Postupalsky (1974). A second nest survey and offspring census was made in mid-August of both years. This latter flight was timed to coincide with the pre-fledging developmental stage of juvenile Ospreys. Immature Ospreys close to or capable of flight were counted (Dunstan 1973). Ground checks were conducted on 17 of the 24 nests each year to confirm the results of the aerial survey.

Nest Site Characteristics.-- We examined nest site characteristics including tree species used, distance of nest from foraging site, proportion of nests located in beaver ponds, and average lifespan of nests. This information was obtained from 1973-1986 Voyageurs National Park records.

1985-1986 Population Data.--Aerial censusing in conjunction with ground checks provided information enabling an estimation of reproductive success (fledglings/pair). In nests monitored from the ground it was also possible to estimate the number of young fledged as a proportion of nestlings. Number of nestlings was determined within the first week of hatching. It was not possible to determine the number of young that actually hatched because there was no access into the nest.

Patterns of Osprey reproductive success were examined to identify differences among the three Park regions. Statistical analysis of 1985-1986 data included both one-way and two way analyses of variance and were performed by SAS (1985) at the University of Minnesota, Duluth. One-way analyses of variance for unequal sample size (Sokal and Rohlf 1981) were used to test the data for significant differences among regions in the following characteristics: number of occupied nests, number of nestlings, number of fledglings, reproductive success, and percent of nestlings fledged. We assumed no interaction between year and region. Because year effect was

insignificant (based on a two-way analysis of variance), years were used as replicates in the one-way analysis of variance of regions. Data were transformed to $\sqrt{X + 1/2}$ and to $\arcsin \sqrt{X}$ as appropriate to ensure a normal distribution of the data. Tukey-Kramer contrasts for unplanned comparisons were performed to identify the differing regions.

1973-1986 Population Data.--Reproductive and distributional data from Park records (Lee Grim 1973-1986, unpubl. data) were combined with data collected during the present study. These data were analyzed using linear regression as described by Sokal and Rohlf (1981) to determine if a relationship existed between years and the following variables: number of occupied nests, number of fledglings, and reproductive success. Analyses were done for each region and for the Park as a whole. Data were transformed to $\sqrt{X + 1/2}$ to ensure a normal distribution. However, data are presented untransformed in the Results for better clarity.

Nest Attendances.--A time budget was recorded for both adult Ospreys at each nest site. Data collected included time spent on nest (nest attendance), near nest site (not on nest), and absent from nest site. A record of nest events was also maintained.

Historical Perspective.--A literature survey was conducted to summarize reproductive success and estimates of breeding pair density obtained in other studies in relatively similar ecological areas. Insufficient records were available to reconstruct natural densities of Ospreys in the area now included in Voyageurs National Park during presettlement times. Because Osprey density appears to be related to beaver density, we obtained data on beaver pond density in the Voyageurs National Park area from about 1940 to present. Using information on beaver density, knowledge of the local fur trade, and present Osprey population trends in Voyageurs, we speculated on the probable Osprey population before European Settlement in this area.

Future Population Trends.--A stochastic model was used to predict how different levels of human disturbance may influence the growth of the Park's Osprey population. The population statistics were manipulated to simulate responses to varying degrees of human disturbance in Voyageurs. The computer program used was the MODUS1 demographics package written by Walt Conley of New Mexico State University (1975).

Demographic data obtained during the summer of 1985 were used as input for the model. Additional data needed for the simulation were derived from the Osprey literature. Data used included: (1) Clutch size: 2.58 eggs/nest (Van Daele and Van Daele 1982); (2) Age-dependent fertility rate: most Ospreys remain in their wintering grounds through their second year (Bent 1937, Henny and Wight 1969); breeding generally begins at age three (Henny and Wight 1969); (3) Age distribution: obtained from a composite life table constructed by Henny and Wight (1969) from band returns of Ospreys banded as nestlings in New York and New Jersey; (4) Survival rate: mortality is greatest during the first year (approximately 50%); in all age classes above one survival rate is 0.838 (Henny and Wight 1969). Immigration and

emigration were not considered in the model; we assumed they offset each other.

The model was further based on the following information: (1) Henny and Wight (1969) used band returns to calculate that New York and New Jersey Ospreys must produce 0.95-1.30 young/breeding age female/year to balance mortality. For modeling purposes, mortality in adults of the Voyageurs population was assumed to equal that of the New York and New Jersey populations. (2) A study by Swenson (1979) in Yellowstone National Park demonstrated that the reproductive success of Ospreys greater than 1 km from a campsite (Type A nest) was four times higher than the reproductive success of Ospreys less than 1 km from a campsite (Type B nest).

We used the model to manipulate the reproductive success of the Voyageurs Osprey population. A reproductive rate of 1.3 was assigned to all Type A nests, and a value of 0.31 (1/4 of the value of 1.3) to all Type B nests. Initially we categorized 24 nests as Type A to simulate the 1985 Voyageurs Osprey population. During the first run four nests were placed into the Type B category leaving 20 Type A nests. This procedure was repeated for a total of six runs placing an additional four nests into the Type B category each time until only one nest was Type A and 23 were Type B. Each run was carried out to 15 years. This procedure allowed us to predict how much human disturbance the park population can tolerate.

Foraging Behavior.--To determine whether there is a difference in foraging behavior among Osprey pairs using different regions of the Park, we examined the following variables:

- (1) Fish species in Osprey diet: Species identity was noted whenever possible while a bird was in flight. In addition, large fishing nets were placed on land under two accessible nests in the Kabetogama region (Wood Duck Island and West Labonty's Pond). Remains of fish that fell or were dropped from the nest were collected and sent to Mona Colburn, Illinois State University, for analysis.
- (2) Dive success: To determine Osprey dive success (fish/dive) we recorded the number of fish captured compared to the number of dives made for each region in Voyageurs, and for the Park as a whole.
- (3) Fish length: During observation periods in 1985 and 1986, we recorded the length of each fish delivered to the nest. Length was estimated by subjectively comparing size of each fish to the body of the adult Osprey. A two-way analysis of variance for unequal sample sizes was used to test for significant differences among regions of the Park.
- (4) Number of fish delivered/hour: During observation periods in 1985 and 1986, the number of fish delivered to the nest was also recorded. Subsequently an average number of fish delivered/hour

was determined for each region in each year. A two-way analysis of variance for unequal sample sizes was used to test data for significant differences among regions of the Park.

- (5) Characteristics of foraging area: We characterized the site where each dive (both successful and unsuccessful) was made by measuring the following variables: (a) light penetration (secchi disk), (b) water depth and (c) distance from nest.
- (6) Foraging time budget: A time budget was constructed for each occurrence of an Osprey foraging. It began when a bird was sighted, included at least one successful or unsuccessful dive attempt, and terminated when the bird returned to the nest or was lost from sight. Each time budget included the following data: (a) total distance traveled, (b) time spent traveling (flying to, between, and from foraging sites), (c) time spent perching, (d) time spent searching (actively looking for fish), (e) time spent eating (away from nest), (f) total time of foraging incident. Statistical analyses were not conducted on these variables because sample sizes were small, and birds were difficult to follow in certain directions with the boat.

Measurement of Water Level Fluctuation

The Lake of the Woods Control Board provided detailed records of water level fluctuations in the four major lakes of the Park; these were obtained from Park Headquarters.

Measurement of Fish Productivity

National Park Service and Minnesota Department of Natural Resources records (1973-1986) of fish productivity (based on catches in standard gang gill nets) were used to estimate lake productivity (Kallemeyn 1985). Nets were 76.2 m long and 1.8 m wide; each contained five 15.2 m long sections. Mesh size varied among sections ranging from 1.9 cm to 5.1 cm. As a measure of lake productivity we used relative abundance of fish as determined by catch per unit effort (CPUE) in standard gang gill nets. The regions were ranked accordingly.

Measurement of Human Disturbance

We obtained data on human activity in the vicinity of nests from Park records of visitor use (Kallemeyn 1985). To supplement Park Service information, we collected data on human disturbance during intensive nest observations (4-6 hr/week) from mid-June to mid-August in 1985, and (8-12 hr/week) from early June to late August in 1986. We focused on quantity of human activity and type of disturbance by determining the following during each observation period: (1) How many people came within 1 km of the nest? (2) What was the purpose of their activity? (3) What was the duration of their activity? and (4) How did each bird respond?

RESULTS

Osprey Biology

Osprey Abundance and Distribution.--There were 24 occupied nests in Voyageurs National Park in both 1985 and 1986, indicating a current breeding population of at least 48 adult Ospreys (Figure 1).

The number of nests in the Park was greater in 1985 and 1986 than in previous years, but their distribution among regions tended to be similar (Table 1). Regional patterns of distribution indicate preferences for particular areas in the Park. Nests within sites may change, but generally are reused. There are three areas of nest concentrations including several large bays off Grassy Bay in Sand Point Lake, east Kabetogama Lake, and west Kabetogama Lake extending into Black Bay of Rainy Lake (Figure 2).

Table 1. Abundance of occupied Osprey nests by region in Voyageurs National Park, 1973-1986.

Year	Kabetogama	Rainy	Namakan/Sand Point	Total
1973	6	3	2	11
1974	2	2	3	7
1975	1	4	3	8
1976	5	3	4	12
1977	6	1	5	12
1978	4	2	4	10
1979	4	3	6	13
1980	5	4	5	14
1981	6	4	5	15
1982	7	4	4	15
1983	8	8	6	22
1984	8	8	6	22
1985	8	8	8	24
1986	9	9	6	24

Nest Site Characteristics.--From 1973 to 1986 nests were recorded in the following species of trees: Black Spruce (Picea mariana) (4), Ash (Fraxinus spp.) (11), Aspen (Populus spp.) (1), American Elm (Ulmus americana) (1), White Pine (Pinus strobus) (4), Red Pine (Pinus resinosa) (5), White or Red Pine (5), and unknown (43). It appears that a wide variety of tree species are suitable for Osprey nests. The major prerequisite is that the tree be dead or dying with the uppermost branches exposed. Nests were typically built at the top of a tree on the trunk. We were unable to determine regional differences in tree species that were used.

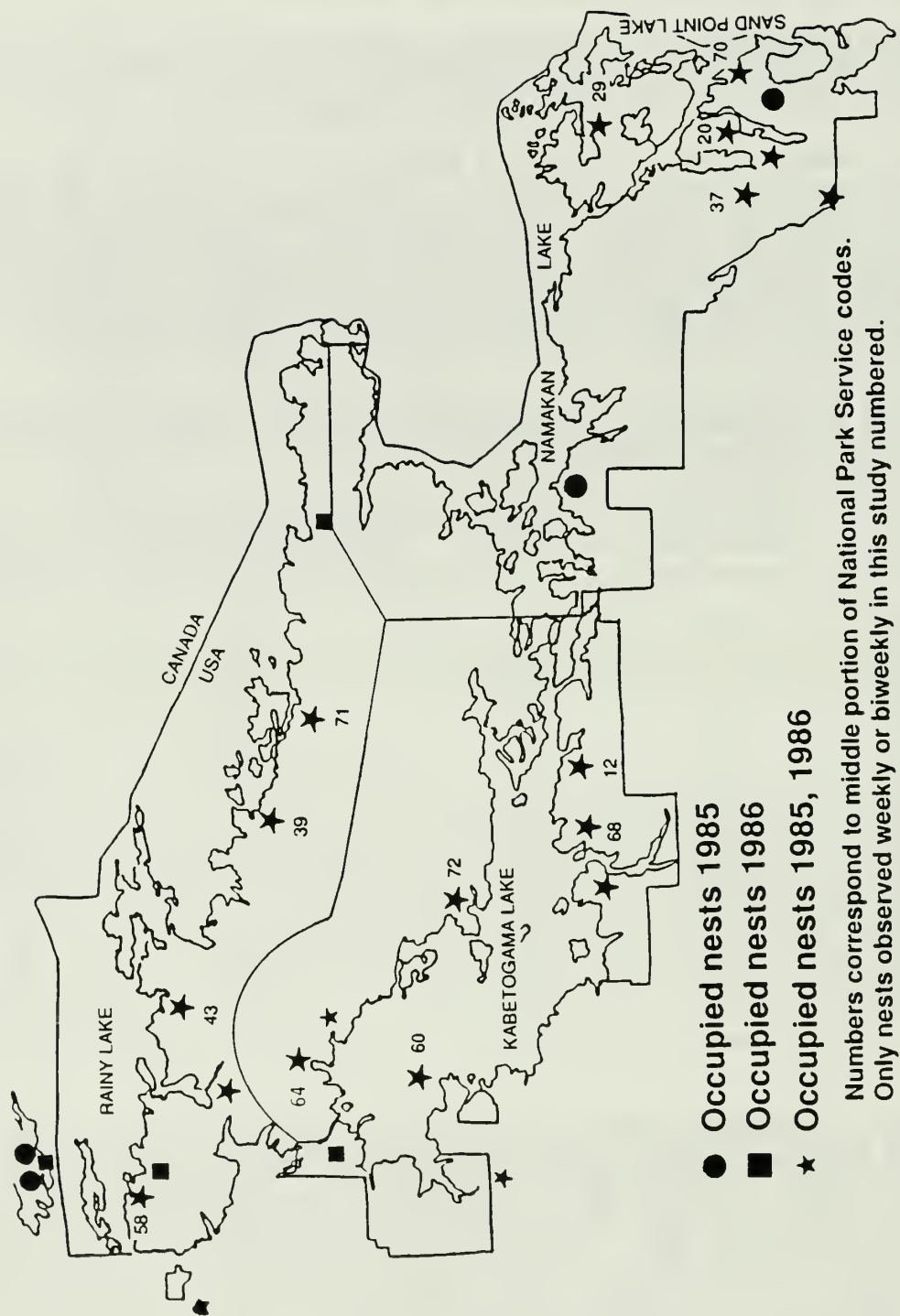


Figure 1. Locations of Osprey nest sites in Voyageurs National Park, 1985-1986.

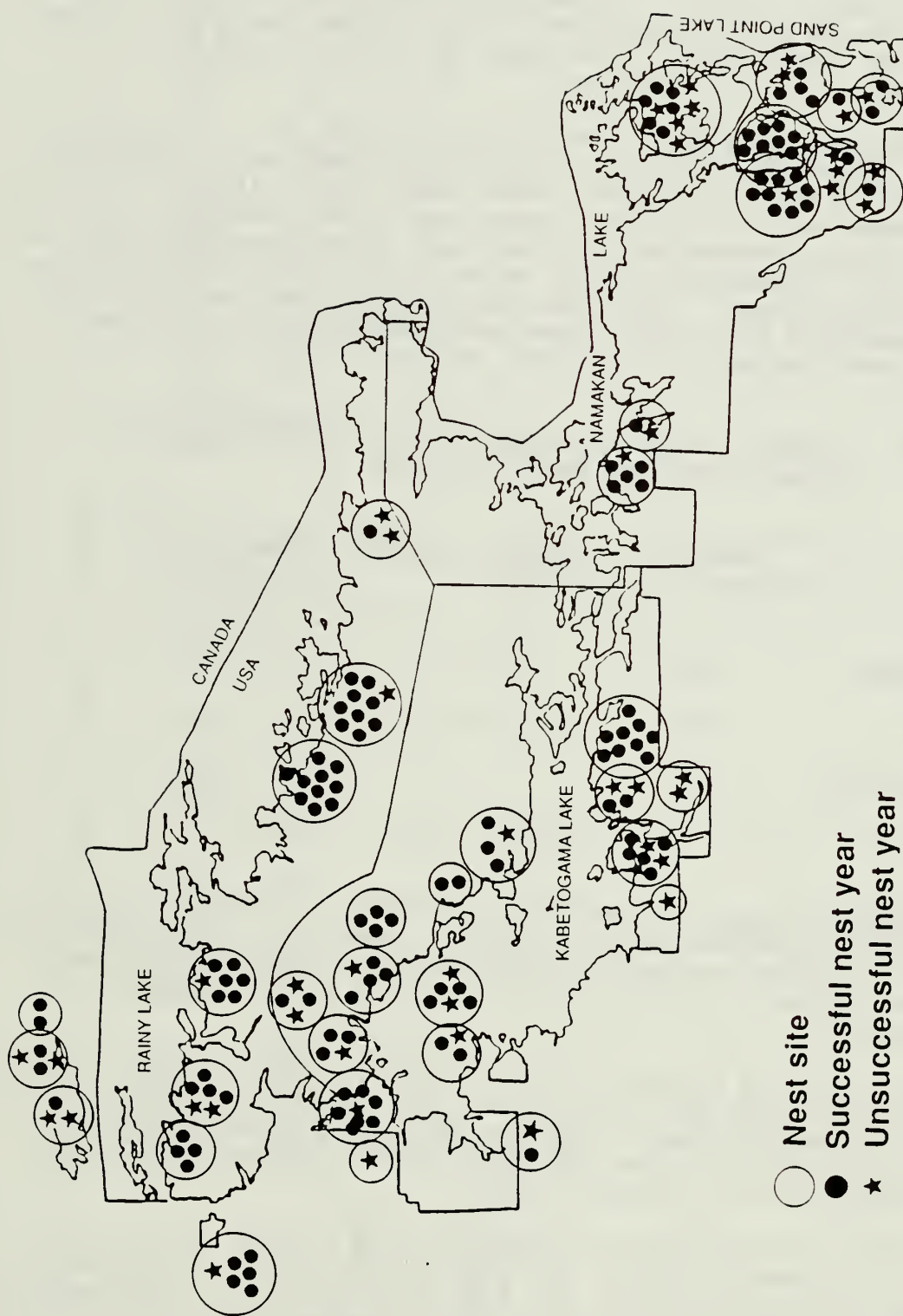


Figure 2. Osprey nest sites in Voyageurs National Park, 1973-1986.

Osprey distribution appears to be influenced by nest site availability as created by beaver activity. Seventy-eight percent of all nests from 1973-1986 were in beaver ponds located from 0.1-2.4 km from a main lake (assumed to be the major foraging site). The remaining 22% were located on islands either on the main or on inland lakes.

Nests were used by Ospreys from 1-14 years (Table 2). Two-way analysis of variance for unequal sample size indicated that there was a significant difference in the average lifespan of nests among regions ($F=3.23$, $P < 0.05$). The Tukey-Kramer test for unplanned comparisons further indicated significant differences between Namakan/Sand Point and each of the other two regions at the 0.05 level. Kabetogama and Rainy did not differ significantly from one another at the 0.05 level. It appears that although fewer nests have been used in Namakan/Sand Point Lakes, these nests have been used during more breeding seasons than nests in the other two areas.

Table 2. Average lifespan of occupied Osprey nests by region in Voyageurs National Park, 1973-1986.

Region	Number of nests	Range of years in existence	Mean years in existence
Kabetogama	25	1-14	3.12
Rainy	18	1-11	3.44
Namakan/Sand Point	12	1-13	5.43

Reproductive Success.--In both 1985 and 1986, the number of occupied nests in Voyageurs National Park was similar. There was a higher degree of variation in the other reproductive characteristics (Table 3). The mean reproductive success for the entire Park over this period was 1.04 fledglings/pair.

In 1985, 28 young fledged from the original 24 occupied nests, 62.5% of these produced at least one fledgling/pair, and reproductive success for the Park was 1.17 fledglings/pair. Seventeen of the 24 occupied nests were monitored throughout the season, and field personnel counted 26 nestlings; eighteen (69.2%) of these fledged (Table 3).

In 1986, 22 juvenile Ospreys fledged from the original 24 occupied nests, 62.5% of these produced at least one fledgling/pair, and reproductive success for all Voyageurs Ospreys was 0.92 fledglings/pair. Seventeen of the 24 occupied nests were monitored throughout the season, and field personnel counted 25 nestlings; nineteen (76%) of these fledged (Table 3).

Table 3. Reproductive Characteristics of Ospreys in Voyageurs National Park, 1985-1986.

Region	Occupied Nests		Number of Fledglings		Nests Fledging Young (%)		Reproductive Success (fledglings/pair)		Occupied Nests with Known Results		Number of Nestlings		Nestlings Fledged (%)	
	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
Kabetogama	8	9	9	11	62.5	66.7	1.12	1.22	7	7	14	12	57.1	91.7
Rainy	8	9	15	9	87.5	77.8	1.88	1.00	4	5	8	8	100.0	75.0
Namakan/ Sand Point	8	6	4	2	37.5	33.3	0.50	0.33	6	5	4	5	50.0	40.0
Voyageurs	24	24	28	22	62.5	62.5	1.17	0.92	17	17	26	25	69.2	76.0

There were no significant differences among Park regions in nest occupation ($F=1.49$, $P>0.10$), number of chicks fledged ($F=8.43$, $P>0.05$), percent of nestlings that fledged ($F=2.15$, $P>0.10$), or reproductive success (fledglings/pair) ($F=5.37$, $P>0.10$). However, there were significant differences among Park regions in number of nestlings ($F=51.68$, $P<0.005$), and percent of nests that fledged young ($F=37.56$, $P<0.010$). In both cases these differences were between the Rainy and the Namakan/Sand Point regions (0.05 level). There were no differences between the Rainy and Kabetogama regions (0.05 level).

The number of nests in each region of the Park gradually increased over the period 1973-1986, resulting in an increase in the Osprey population of Voyageurs National Park (Figure 3). There was a corresponding increase over the years 1973 -1986 in the numbers of fledglings in all regions except Namakan/Sand Point (Figure 4). Reproductive success increased over the years 1973-1986 only in the Kabetogama region (Figure 5). It varied inter-annually from 0-2 fledglings/pair (Figure 5), and averaged 0.98 fledglings/pair for all regions of the Park over these years (Table 4).

Table 4. Reproductive characteristics of Osprey by region in Voyageurs National Park, 1973-1986.

Region	Nests	Number of Fledglings	Nests Fledging Young (%)	Reproductive Success (fledglings/pair)
Kabetogama	79	79	57	1.00
Rainy	63	71	69	1.13
Namakan/ Sand Point	67	55	58	0.82
Voyageurs	209	205	61	0.98

Nest Attendance.--During weeks 1-5 of the nestling period (the first or second week of June through the first or second week of July) females were on the nest over 90% of the time. At week 6 (second or third week of July) a marked decline in female nest attendance began. Fledging occurred during week 8 (the last week of July or first week of August). At this time females were on the nest only 30% of the time. At week 9 (first or second week of August) females attended nests 10-20% of the time. During weeks 10-12 (second or third week of August - fourth week of August) female nest attendance was from 0-5% (Figure 6). Male nest attendance was generally low ranging from 5-30% during the first 4 weeks of the nestling period, and 0-10% during weeks 5 and 6. Males almost never attended nests after week 6.

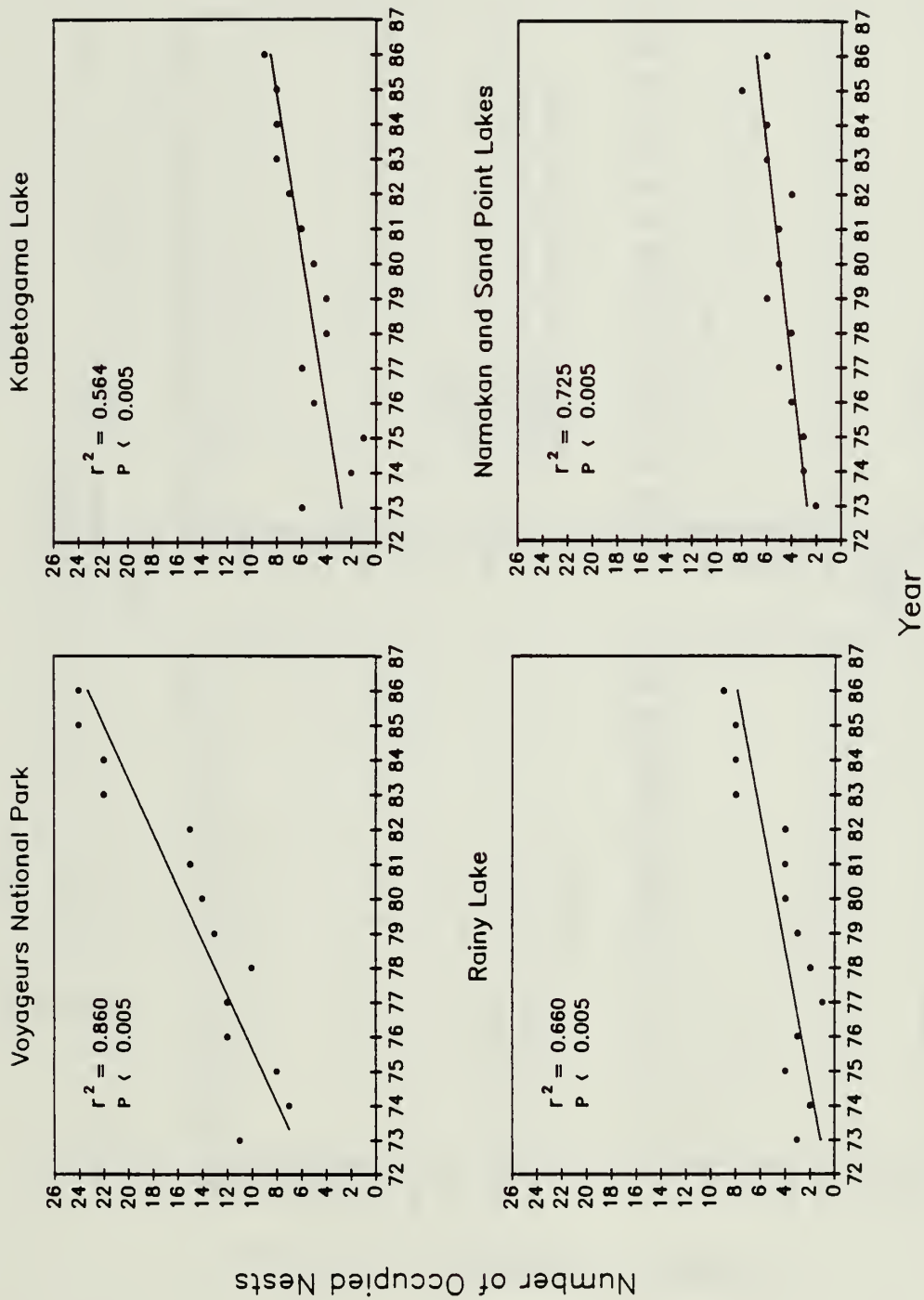


Figure 3. Relationship between years and number of occupied Osprey nests by region in Voyageurs National Park, 1973-1986.

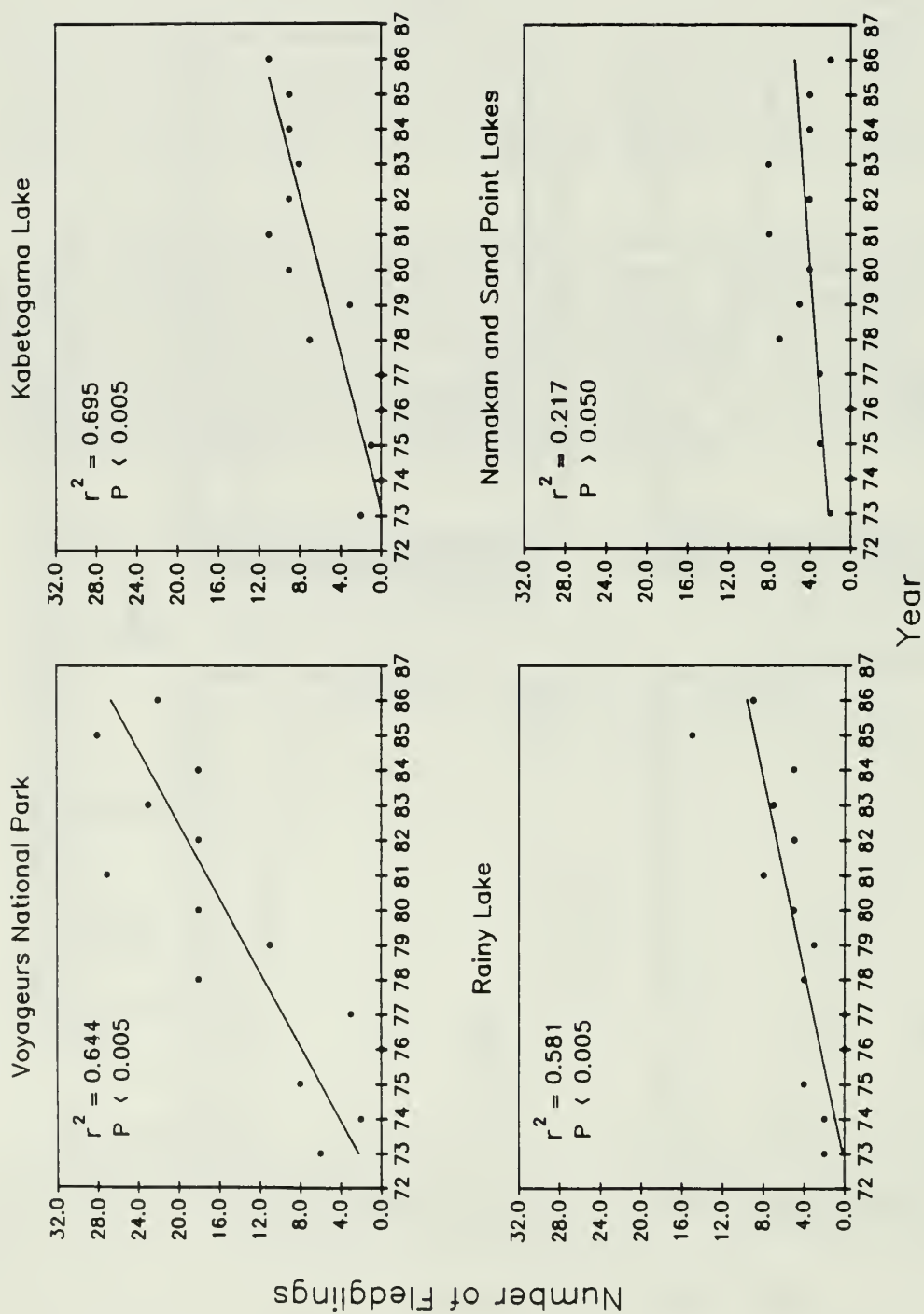


Figure 4. Relationship between years and number of Osprey fledglings by region in Voyageurs National Park, 1973-1986.

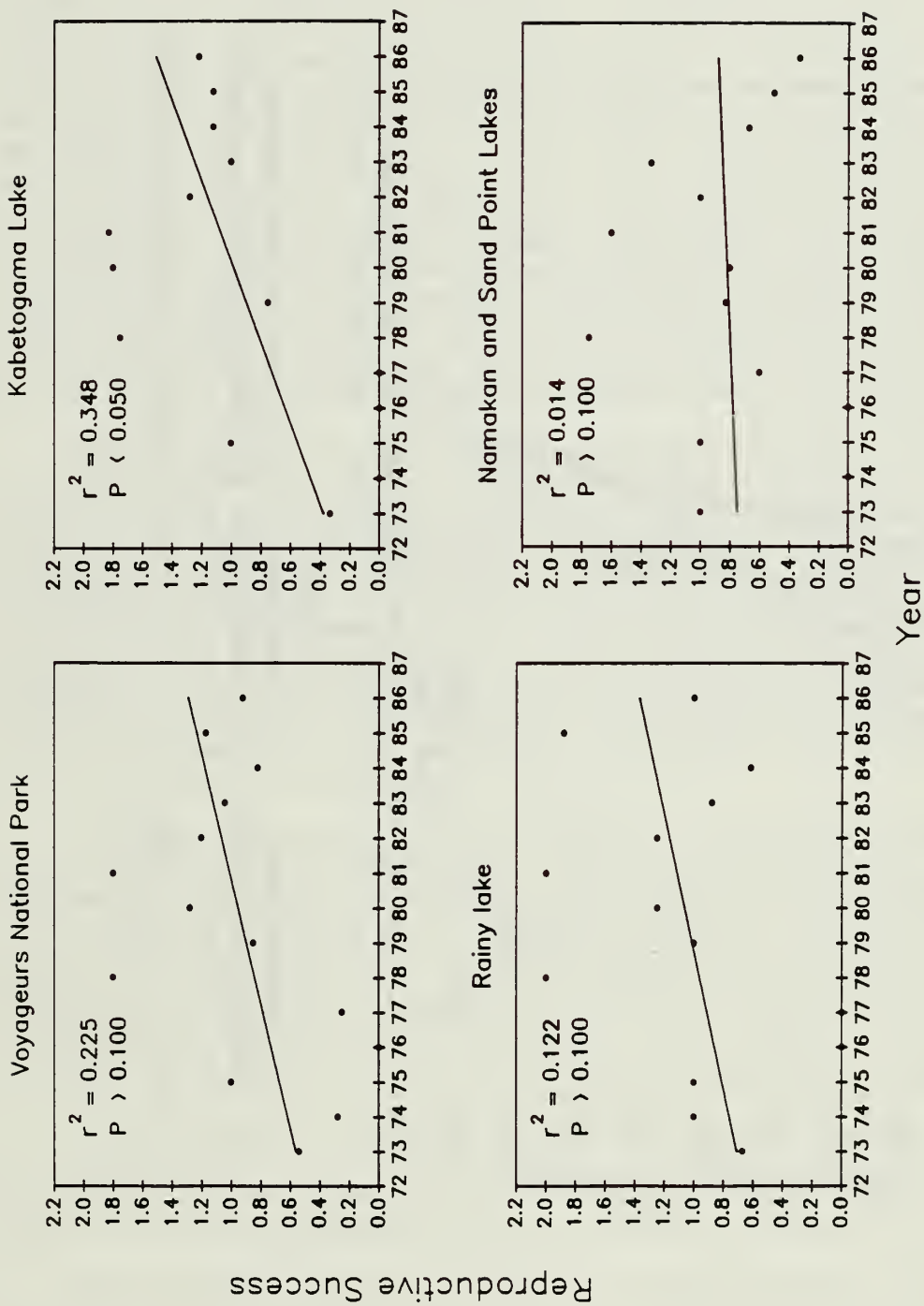


Figure 5. Relationship between years and Osprey reproductive success (fledglings/pair) by region in Voyageurs National Park, 1973-1986.

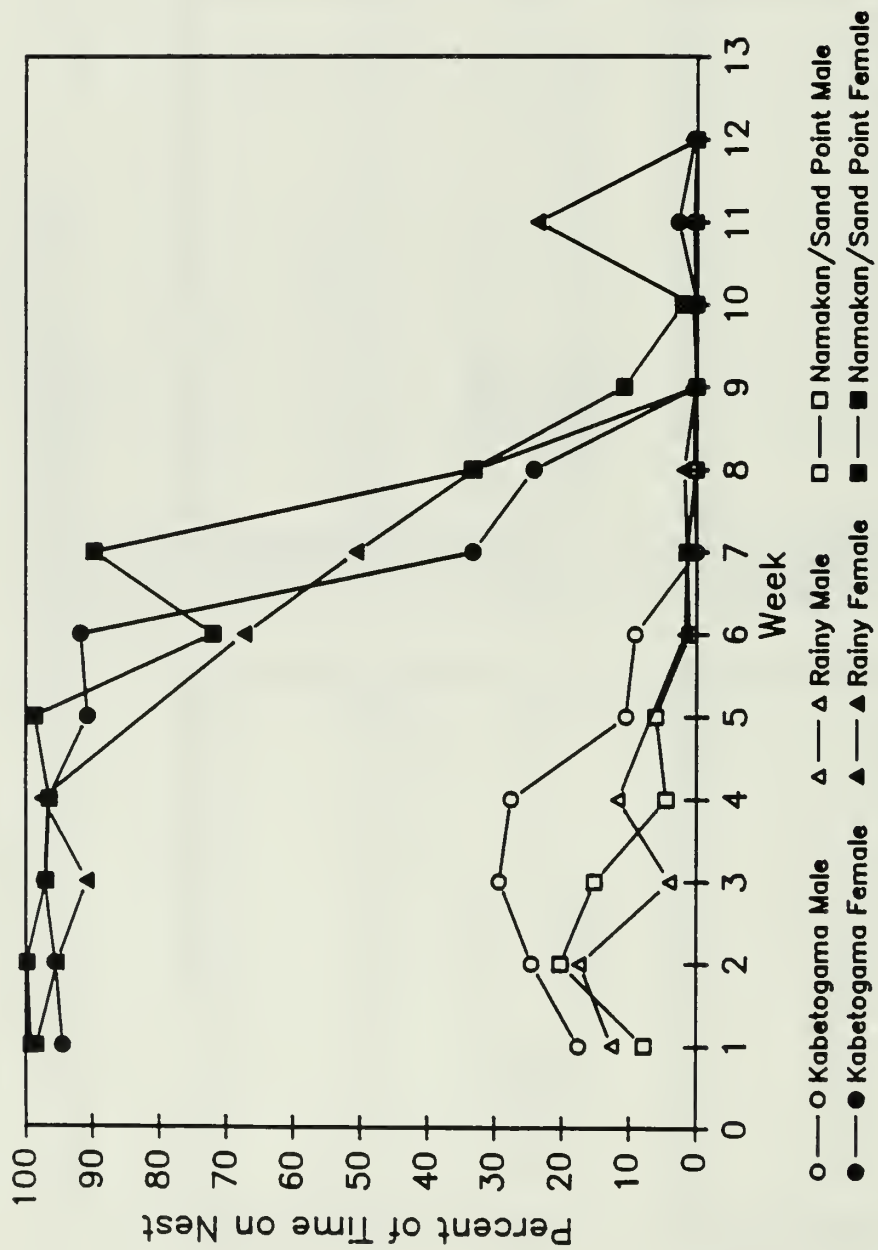


Figure 6. Time budget of nesting Ospreys by region in Voyageurs National Park, 1986.

Future Trends.--Results of the computer simulation used to predict response of the Voyageurs Osprey population to different levels of human disturbance are summarized in Figure 7. A reproductive rate of 1.30 from 24 Type A nests (campsite > 1 km from nest) caused the population to almost quadruple after 15 generations (24-92.7 pairs). A reproductive rate of 1.13 from 16 Type A nests and 8 Type B nests (campsite < 1 km from nest) caused the population to approximately triple after 15 generations (24-81 pairs). A reproductive rate of 0.96 from 12 Type A nests and 12 Type B nests caused the population to slightly more than double after 15 generations (24-55.1 pairs). A reproductive rate of 0.78 from 8 Type A nests and 16 Type B nests caused the population to almost double after 15 generations (24-44.5 pairs). A reproductive rate of 0.61 with 4 Type A nests and 20 Type B nests caused the population to remain nearly constant, but showed a downward trend after 15 generations (24-26.8 pairs). And finally, in the sixth run a reproductive rate of 0.44 with 1 Type A nest and 23 Type B nests caused the population to decline by more than half after 15 generations (24-10.3 individuals).

Foraging Behavior.--Analysis of fish remains at nests revealed that the following species were present in the Osprey diet: northern pike (Esox lucius), yellow perch (Perca flavescens), sauger (Stizostedion canadense), white sucker (Catostomus commersoni), largemouth bass (Micropterus salmoides), lake whitefish (Coregonus clupeaformis), longnose sucker (Catostomus catostomus), and burbot (Lota lota). In addition, some remains were identified to genus only. These were most likely, walleye (Stizostedion vitreum), cisco (Coregonous artedii), and smallmouth bass (Micropterus dolomieu). Bones from northern pike (n=17) occurred approximately three times more frequently in the sample of fish remains than did any other species, followed by yellow perch (n=5). All other species were identified only once or twice in the sample.

Dive success ranged from 1 fish/dive to 1 fish/5 dives and there were no significant differences among regions ($F=3.07$, $P>0.05$) (Table 5). There also were no differences among regions in length of fish captured by Ospreys ($F=0.66$ $P>0.10$) (Table 6). The year effect for fish length may have been obscured by the unsystematically large standard deviation found in the Namakan/Sand Point region in 1985. The rate of fish delivered to nests was marginally not significant among regions ($F=3.02$, $P=.09$) (Table 7); regional differences may have been detectable if a larger sample size had been available for analysis.

Foraging sites in Voyageurs National Park can be characterized as shallow areas with light transmittance to an average depth of 1.20 m (Table 8). Although birds tended to forage relatively close to their nest site, Ospreys from west Kabetogama Lake also foraged in Black Bay of Rainy lake.

There was great variation in Osprey foraging behavior (Table 9, Figure 8). Time spent foraging ranged from four minutes to just over three hours. Total distance traveled from nest to return ranged from 1-25 km. Travel time to, between, and from foraging sites ranged from 1-50 minutes. Time spent perching while foraging ranged from 0-2.5 hours. Searching for prey ranged from 1 minute - 1.2 hours. Eating while foraging ranged from 0-3.1 hours.

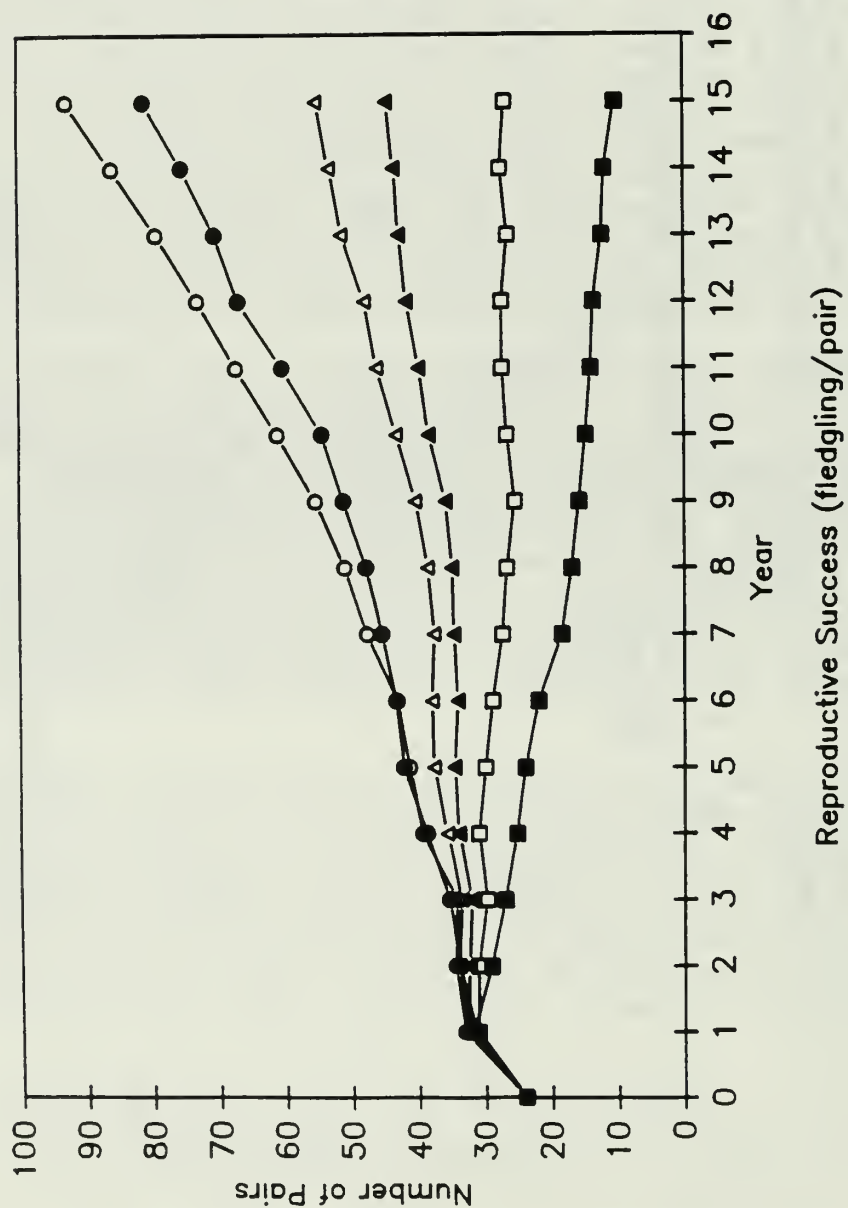


Figure 7. Computer simulation of change in an Osprey population (N=24) based on differential reproductive success over a period of 15 years.



Figure 8. Osprey foraging time budget by region in Voyageurs National Park, 1986.

Table 5. Osprey dive success by region in Voyageurs National Park, 1986.

Region	Number of Dives	Dive Success (fish/dive)
Kabetogama	66	0.47
Rainy	41	0.54
Namakan/ Sand Point	16	0.31
Voyageurs	123	0.47

Table 6. Comparison of length ($\bar{x} \pm SD$) of fish captured by Ospreys from different regions in Voyageurs National Park, 1985-1986.

Region	Nests (1985)	1985 $\bar{x}$ length (cm)	Nests (1986)	1986 $\bar{x}$ length (cm)
Kabetogama	4	22.9 $\pm$ 3.0	4	20.5 $\pm$ 1.1
Rainy	4	23.4 $\pm$ 2.6	2	20.3 $\pm$ 2.2
Namakan/ Sand Point	3	27.5 $\pm$ 8.8	2	20.8 $\pm$ 1.2

Table 7. Number of fish delivered to nest/hour ($\bar{x} \pm SD$) by region, 1985-1986.

Region	Fish/hour 1985	Fish/hour 1986
Kabetogama	0.26 $\pm$ 0.29	0.32 $\pm$ 0.01
Rainy	0.41 $\pm$ 0.40	0.44 $\pm$ 0.05
Namakan/Sand Point	0.24 $\pm$ 0.27	0.24 $\pm$ 0.02

Table 8. Characteristics of Osprey foraging areas by region in Voyageurs National Park, 1986.

Region	Secchi Disk (m)	Depth (m)	Distance from Nest (Km)
Kabetogama	1.30	2.30	1.95
Rainy	1.04	1.50	3.00
Namakan/Sand Point	1.23	1.80	4.50
Voyageurs ($\bar{x}$)	1.20	1.96	3.88

Table 9: Average values of Voyageurs National Park Osprey foraging time budget by region, 1986.

Region	Distance (km)	Travel (min)	Perch (min)	Search (min)	Eat (min)	Total (min)
Kabetogama	7.25	7.32	23.64	17.28	9.54	57.72
Rainy	7.38	3.90	3.36	18.72	0.00	25.98
Namakan/ Sand Point	5.33	9.00	21.78	14.58	19.92	65.40
Voyageurs	7.08	7.10	19.61	17.47	13.00	57.18

Lake Productivity

Based on standard gill net catches, the six most abundant fish species in Voyageurs National Park lakes are: walleye, cisco, yellow perch, sauger, white sucker and northern pike (Figure 9). Generally, the region with the greatest number of a particular species also had the greatest biomass of that species (Figure 10). Park regions ranked in the following order in terms of relative abundance as determined by CPUE: Kabetogama, Rainy, Sand Point, and Namakan.

Littoral percentages vary among the Voyageur lakes. Rainy Lake has a surface area of 893.87 km² and a littoral zone (shallow water, 4.6 m and less) of 312.85 km². The portion of Rainy Lake considered in this research

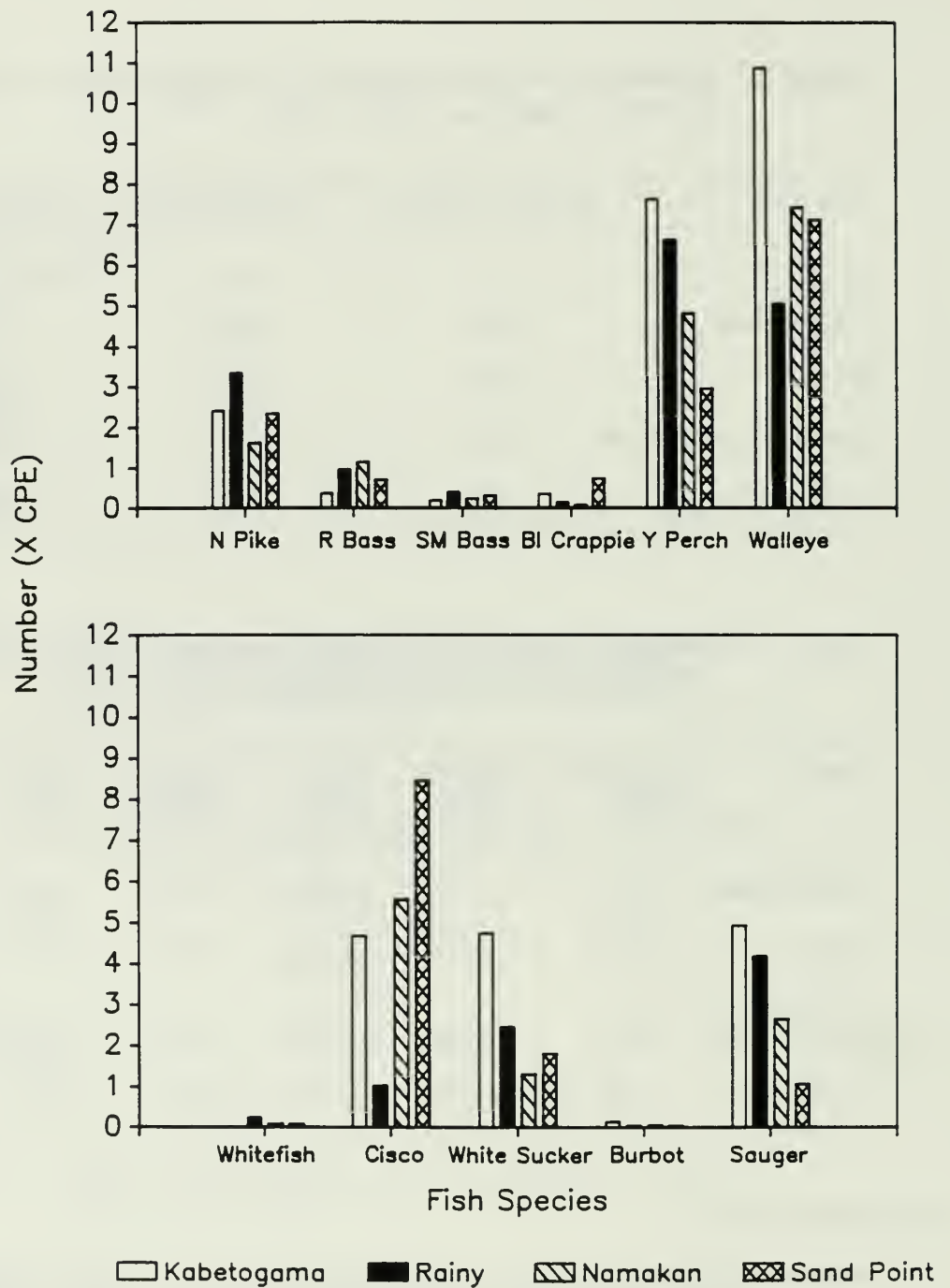


Figure 9. Relative fish abundance based on the average number of fish caught in experimental gillnets in four lakes in Voyageurs National Park, 1973-1986.

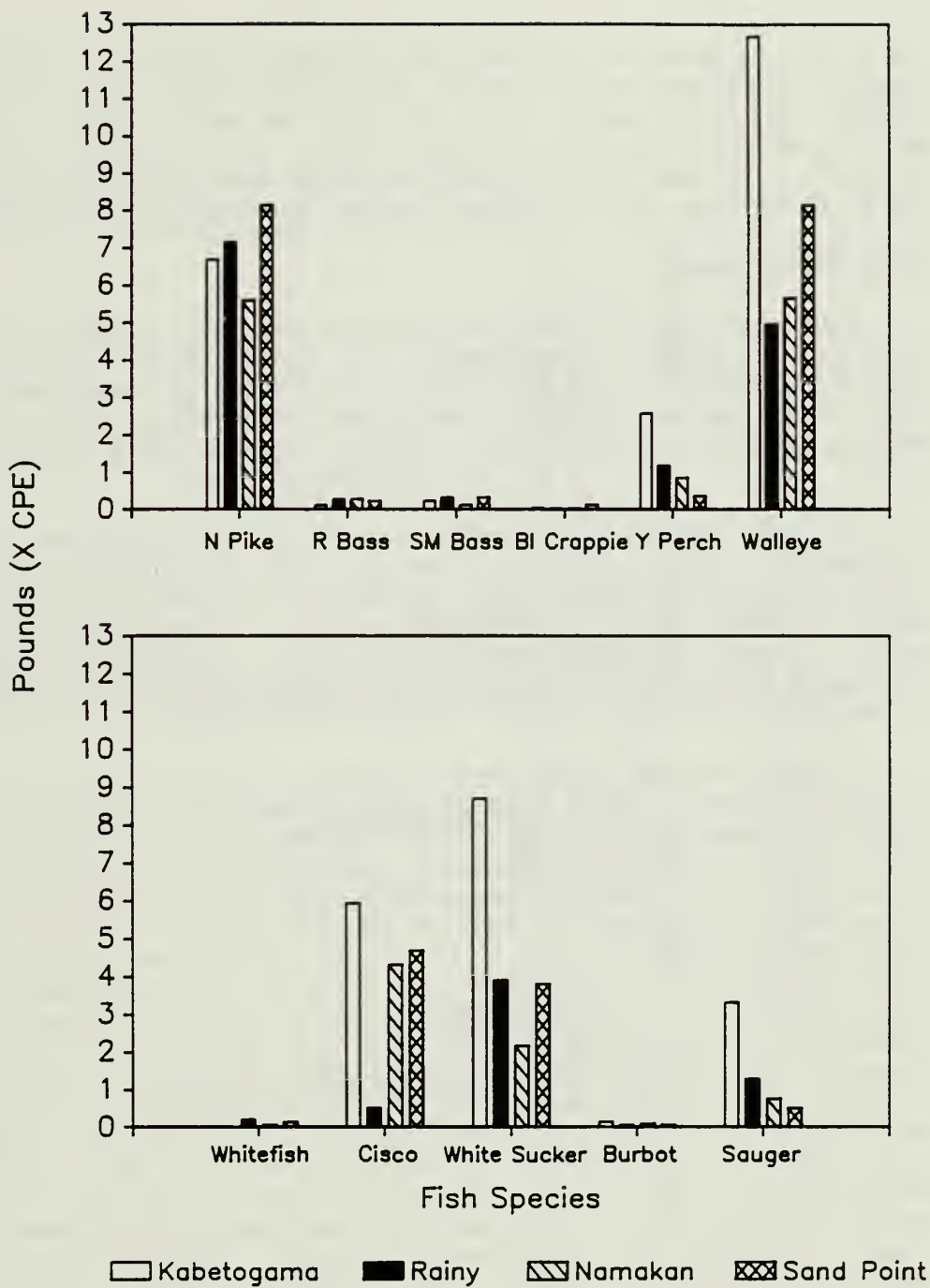


Figure 10. Relative fish abundance based on the average weights of fish caught in experimental gillnets in four lakes in Voyageurs National Park, 1973-1986.

has a surface area of 76.68 km² and a littoral zone of 26.8 km². Kabetogama Lake has a surface area of 104.21 km² and a littoral zone of 31.26 km². Namakan Lake has a surface area of 114.83 km² and a littoral zone of 22.97 km². Sand Point Lake has a surface area of 35.98 km² and a littoral zone of 11.5 km². The most extensive shallow water area used by Ospreys was Black Bay of Rainy Lake with a surface area of approximately 22.6 km².

Human Disturbance

Four categories of potential human disturbance were observed: (1) aircraft, (2) canoe, (3) motorboat, (4) person on foot. Most disturbances lasted 1-2 minutes. However, two nests situated on Kabetogama Lake (Wood Duck Island and West LaBonty's Pond) were frequently subject to longer periods of human activity such as people fishing from a motorboat near the nest.

The most prevalent form of human activity near nests was aircraft (Figure 11). This greatly exceeded any other type of human activity in all regions except Kabetogama Lake. Motorboats were the second most frequent source of potential disturbance (Figure 11). In Kabetogama Lake motorboat traffic slightly exceeded aircraft activity. In the Namakan/Sand Point Lakes motorboats were not a potential source of disturbance. Disturbance by canoes or people on foot was low in all areas of the Park.

Osprey responses to human disturbance typically consisted of: (1) one or both adults turning their head to look at the source of sound or, (2) no obvious response (Figure 12). Other responses, including agitation (frequent head turning, pre-flight movements) and vocalizations, occurred less than 5% of the time in all regions (Figure 12). Human disturbances occurred approximately 0.5 times per hour at maximum (aircraft on Rainy Lake), and we interpreted Osprey responses to be minimal. Ospreys were most sensitive to disturbances that occurred within 50-100 m of the nest, regardless of category. Typically, only canoes and people on foot entered this range. However, when disturbance occurred within 50-100 m of a nest site, the attending adult became extremely agitated, vocalized persistently, flew off the nest, circled the area, and often did not return to the nest until 15 or more minutes after the disturbance ceased. Fledglings also became agitated when disturbance occurred in the immediate nest site area. The two Osprey nests subject to the greatest disturbance were located on Wood Duck Island and West LaBonty's Pond. The Wood Duck nest was 15-20 m from shore and 1 km from a developed shoreline (resorts, cabins). Human activity in the form of people fishing from motorized boats, canoeists exploring the shoreline, and occasional float plane activity was constant.

The West LaBonty's Pond nest is located in an inactive beaver pond. It is approximately 0.1 km from the shore overlooking a bay that is frequently fished. Disturbance here is not as great as at Wood Duck Island and can be characterized as motorboat noise and human voices.

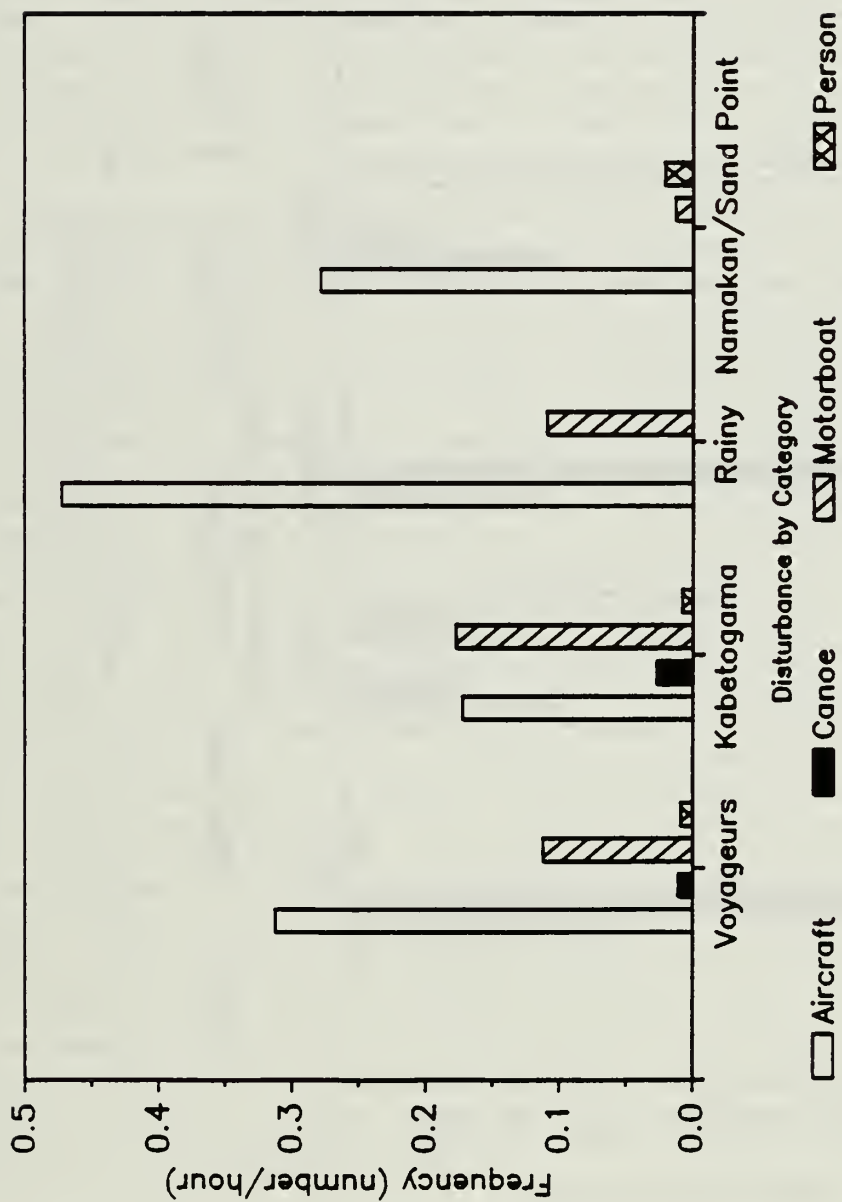


Figure 11. Frequency of potential human disturbance of nesting Ospreys by region in Voyageurs National Park, 1985-1986.

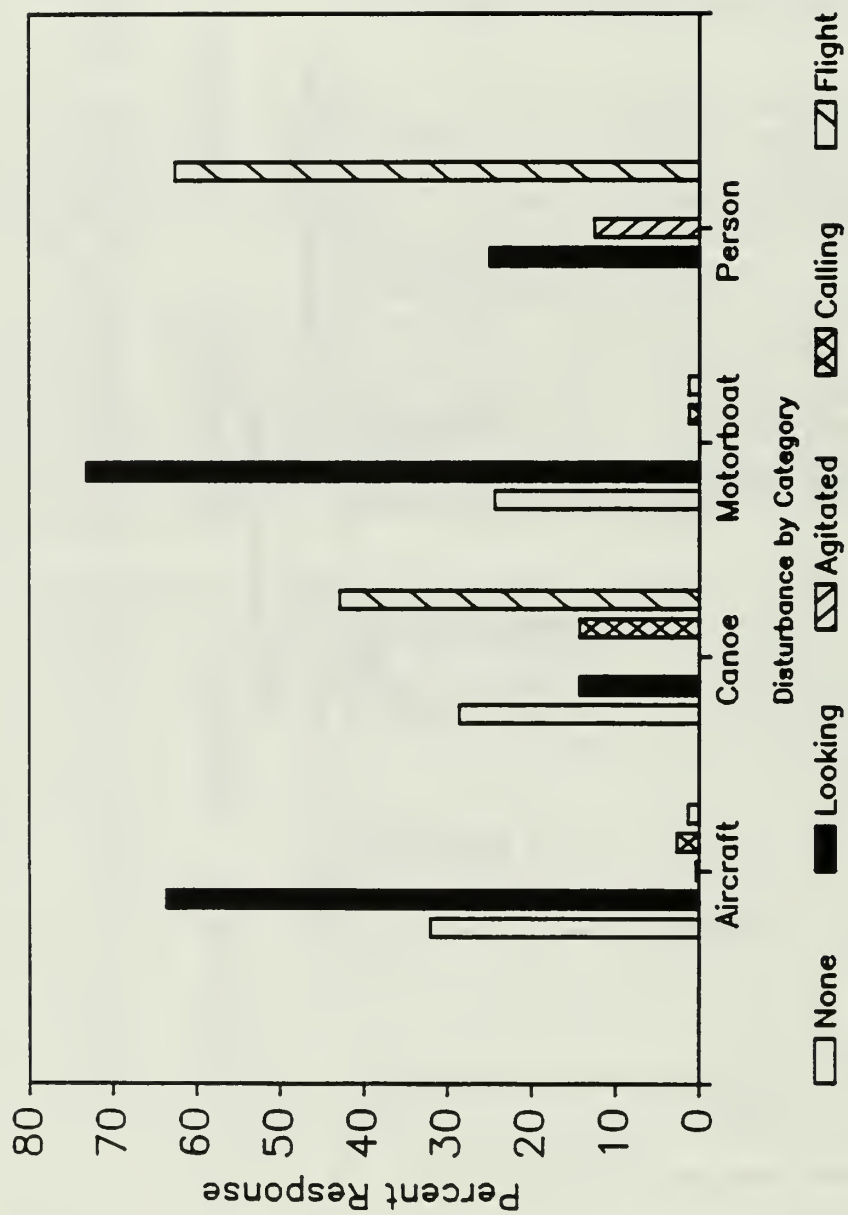


Figure 12. Adult Osprey response to human disturbance of nest sites in Voyageurs National Park, 1985-1986.

DISCUSSION

Osprey Biology

Osprey Abundance and Distribution.--Results of aerial surveys indicate there has been a steady population increase from 11 pairs in 1973 to 24 pairs in 1986. Although improvements in survey techniques may account for some of the increase recorded in the Voyageurs National Park Osprey population size, other factors, such as decreased use of organochlorine pesticides in the United States and an increased beaver population in the Park are almost certainly more important.

Ospreys and pesticide use: According to observations of many ornithologists, the Osprey population in North America began to decline around the beginning of the 20th century (Ames and Mersereau 1964; Henny and Wight 1969). The magnitude of this decline, particularly in the northeastern U.S., greatly increased in the 1950's; this generated considerable concern among conservationists. At the time, this decline was attributed to poor reproductive success caused by human encroachment and environmental contamination of Osprey nesting habitat. Henny and Ogden (1969) examined the magnitude of declining Osprey populations in portions of seven states: Florida Bay, Florida; the eastern shore of central Chesapeake Bay, Maryland; the headwaters of the Wisconsin River in northern Wisconsin; northern Michigan; Louds Island, Maine; 16 Minnesota counties; and the Connecticut River in Middlesex and New London counties, Connecticut. In six of these seven states, the populations appeared to be decreasing. It is noteworthy that the rate of decline in Wisconsin greatly increased from the 1950's to the 1960's. Henny and Ogden (1969) attributed this population change to contamination from accumulation of chlorinated hydrocarbon insecticide residues. They based this conclusion on raptor research that correlated magnitudes of decreases in eggshell weights, decreases in breeding populations, and exposure of populations of raptors to persistent organic insecticides (Ratcliffe 1967; Porter and Wiemeyer 1969; Spitzer et al. 1977). Because DDT was banned in the United States in 1972, these pesticides currently are not a problem for Ospreys at their breeding sites in the U.S. However, it is important to recognize that although the overall use of these chemicals has significantly decreased, they are still in use in Central and South America where many North American Ospreys winter. In conclusion, the discontinued use of chlorinated hydrocarbon insecticides in the United States may have contributed to the increase in the Voyageurs Osprey population, between 1973-1986. At least a portion of this increase appears to be internal to the Park based on the increase in reproductive success of the Kabetogama region over this period.

Beaver activity and Osprey distribution: Osprey distribution in Voyageurs also appears to be influenced by nest site availability, as created by beaver activity in the Park. During our study, Ospreys typically nested in the top of trees killed by high water held behind beaver dams. Based on the current number of beaver impoundments, site availability is probably not currently limiting the Osprey population. However, we do not have information

on the number of ponds with suitable nest trees, or on their distribution throughout the Park.

Nest tree characteristics and Osprey distribution: Records of nest trees indicate that Ospreys appear to be flexible in their use of different tree species. Most nests were not on the main lakes but in beaver ponds up to 2.4 km away. Nest sites were used repeatedly from year to year, probably due to adult fidelity to breeding areas and possibly fidelity of first-time breeders to the general natal area (Newton 1980). While fewer nests were used in the Namakan/Sand Point Lakes, those that were there have had significantly longer lifespans than those in the other areas. It is not clear why this difference exists. We do not have enough information on tree species used to ascertain if there was a regional difference in species selected for nest sites. It is also possible that there are fewer nest trees available in the Namakan/Sand Point Lakes region but we did not collect data to test this hypothesis.

Regional patterns of nest site distribution: The mean number of nests/region from 1985-1986 is similar among regions; the 1985-1986 distribution of these nests within regions is clumped. Nests on Namakan/Sand Point Lakes are located in several large bays off Grassy Bay in Sand Point Lake. Although Kabetogama Lake nests encircled the lake, there were two areas of concentration. One concentration near Kabetogama Narrows had three nests on the south shore off three consecutive bays, and one nest on the north shore. The second concentration was on the west end of the lake (five nests, one on Wood Duck Island). These blended into a concentration of birds around and near Black Bay on west Rainy Lake. The foraging areas of these birds overlapped. There were three nests on east Rainy Lake. Two of these were close to each other and the third was isolated from all other known nests. These isolated nests may be birds that were not able to gain access to better foraging areas. However, there are no data supporting the idea that these isolated pairs use marginal nesting or foraging habitat.

Concentrations of Ospreys in the Park are probably not random, but occur due to local fish productivity and to nest site availability. Water levels most likely influence nest site distribution indirectly through fish productivity. Human disturbance does not currently appear to affect Osprey nest distribution.

Reproductive Success.--Analyses of the data on reproductive success during 1985 and 1986 indicate no significant differences between years for any of the reproductive characteristics examined. However, they do indicate significant differences among regions of the Park for number of nestlings, and for percent of nests fledging young. These differences existed between the Rainy and Namakan/Sand Point regions. We found no regional differences between the number of occupied nests, the number of fledglings, the number of nestlings fledged, and reproductive success (fledgling/pair). Absence of significant differences among regions for reproductive success may be due to a small sample size and low variation in initial clutch size. It is important to consider that the maximum reproductive success reported for any Osprey population is approximately 2 fledglings/pair. Clearly the difference

between 1.44 (mean reproductive success for Rainy 1985 and 1986) and 0.42 (mean reproductive success for Namakan/Sand Point 1985 and 1986) is meaningful. Several interesting trends are evident.

There was a distinct pattern in the reproductive characteristics of 1985. Rainy Lake consistently ranked highest for all categories except occupied nests, where all regions were equal, and in number of nestlings, where Kabetogama Lake ranked highest. The pattern in 1986 was also distinct. Kabetogama Lake consistently ranked highest for all categories except occupied nests, where it was equal to Rainy Lake, and in the percent of nests fledging young, where Rainy Lake ranked highest. In both years there was a relatively large gap in numbers and percentages between the region ranking second and the Namakan/Sand Point Lakes region, which consistently ranked last. The important point here is that while Namakan/Sand Point Lakes started each season with a similar number of occupied nests as the other regions, it consistently ranked lower in all other reproductive success characteristics. From nest site observations, it appeared that nests in this region were abandoned late in the incubation period (late May - early June). The highest nestling mortality occurred in the Kabetogama region. Sibling aggression played a role in this mortality. This behavior may be linked to food stress (Lack 1966; Poole 1979, 1982). Asynchronous hatching is common in many raptor populations (including Ospreys) and is thought to be an adaptation to adjust breeding rates to food supplies that may differ from year to year. Young are born graded in competitive abilities which are based on age differences and elimination of nestlings through starvation. Osprey sibling aggression appears to be reversible and is gauged by hunger levels. This mechanism allows the young sibling(s) to gain proper nourishment in productive conditions (Poole 1982). In Voyageurs National Park intense sibling aggression occurred exclusively in nests of three with only one exception. This was in a nest of two in the Namakan/Sand Point Lakes region. All nests with three nestlings ($n=6$) experienced mortality. Nestling mortality occurred in only two nests where no sibling aggression was noted ($n=11$). Data on reproductive success collected by Grim from 1973-1986 indicate that the Voyageurs Osprey population has increased over these years. The increase in the number of fledglings produced from 1973-1986 corresponded well with the increasing number of occupied nests. However, the Namakan/Sand Point Lakes region did not follow this trend.

Reproductive success (fledglings/pair) did not appear to increase or decrease over the years of 1973-1986 for the Rainy and Namakan/Sand Point regions, or for the Park as a whole. However, there was an increase in reproductive success in the Kabetogama region. The lack of increase in reproductive success in most of the Park may be due to low variation in initial clutch size per nest. Some factor or factors appear to be suppressing reproductive success in Namakan/Sand Point Lakes.

Additional factors not examined in this study may contribute to differences found among regions; these include: (1) local weather conditions, (2) environmental contaminants (e.g., mercury); (3) age-structure, distribution, and behavioral characteristics of fish.

Future Trends.--The results of the population growth simulation indicate that Henny and Wight's (1969) reproductive success range of 0.95-1.30 not only maintains the Osprey population in Voyageurs, but allows for an increase. Both rates of increase are fairly high. At a reproductive rate of 1.3 the population can triple over a period of 15 years. At a rate of 0.96 it can double after 15 years. This demonstrates that reproductive success can be lower than the model indicates and that the Voyageurs Osprey population can probably tolerate a certain level of human disturbance. It is important to keep in mind that this is only a model and merely simulates a situation based on pre-defined variables, providing an idea of what may happen with a certain set of circumstances. The important point is that the Osprey population in Voyageurs National Park appears to be stable. Offspring are being produced and surviving at a great enough rate that the population is currently increasing.

Foraging Behavior.--Osprey foraging areas can be characterized as shallow water areas, generally in bays or around islands. We speculate that Ospreys forage in these regions because they are the preferred habitat of northern pike, their major food item. In addition, light penetration in the large lakes of the Park is low ($\bar{x} = 1.20$ m), limiting visibility. Birds may have a better opportunity to see fish in shallow water as well as to judge the distance of prey from the surface.

Regional differences in diet were not analyzed because fish remains were collected only from the Kabetogama Lake region. However, we believe that the species in these samples are representative of a typical diet of Voyageurs Ospreys.

It was interesting to note that a lake whitefish was recovered at the Wood Duck Island nest, yet this species is not included in the Voyageurs National Park records on fish gill netted in Kabetogama Lake. This discovery provides some evidence that the Wood Duck Island birds also foraged in Rainy Lake, probably Black Bay. In fact, adults from two different Kabetogama nests sites were observed traveling in the direction of Black Bay during a number of foraging observation periods in 1986.

No regional differences were indicated for dive success. However, Ospreys foraging in Namakan/Sand Point Lakes tended to have lower dive success than birds foraging in the other Park regions. These data must be regarded with caution because the sample size was low for the Namakan/Sand Point Lakes.

The dive success rate for the Park (47%) is at the lower range of that reported in other Osprey research. Many studies examining Osprey foraging ecology were conducted in the 1970's in the western U.S., and in Florida. Swenson (1978) reported a dive success rate of 47% for the Yellowstone Lake, Wyoming, Osprey population. At Eagle Lake, Lassen County, California, Garber (1972) found that Ospreys were 56% successful in their fishing efforts. Over a three year period, MacCarter (1972) found Ospreys at Flathead Lake, Montana to be 65% efficient. Several investigators report dive success rates of 80%

and above; these include Ueoka and Koplin (1973) at south Humbolt Bay, California, and Nesbitt (1974) at Newnans Lake, Florida.

Several studies have estimated the lengths of fish captured by Ospreys. Results appear to be similar to those recorded in Voyageurs. Swenson (1978) reported a mean fish length of 28 cm, and Ueoka and Koplin (1973) reported lengths ranging from 18-23 cm.

Much of Osprey foraging research has focused on catch rate of fish. Typically this has been measured by recording the time an Osprey first was sighted until it captured a fish, or was lost to view. Because these populations were high in density and either located adjacent to isolated water sources or concentrated around prime marine foraging areas, quantification of catch rate was possible.

We did not measure catch rate, rather we constructed a time budget which allowed calculation of rate of delivery of fish to nests. We found little reference to fish delivery in other Osprey research. While Jamieson et al. (1982a,b) also looked at rate of fish delivery, they did not look extensively at foraging behavior. They found that males fish continuously returning to nests as soon as fish are caught, possibly spending a few minutes eating part of the fish.

We found tremendous variation in foraging behavior among individual birds. Some habitually made their dives from the same perches rather than from the air, some spent most of their time at the nest, and others perched away from the nest for up to three hours while occasionally eating one or more fish. Travel times and distances also varied. The Osprey foraging time budget is probably most accurate for Kabetogama Lake, where it was easier to follow birds from the nest to return. Observations were difficult in Rainy Lake because most activity was concentrated in Black Bay, and individuals often were impossible to follow for the entire foraging period. In general, male Ospreys at Kabetogama Lake spent more of their time perched at the nest sites. Rainy Lake males spent little time perched, either away from nest sites or while foraging. They seemed to invest more time foraging, both in searching for fish and in the number of trips made. This is reflected in a higher, although not significantly different, number of fish delivered to the nest per hour. Namakan/Sand Point Lake males spent little time perched at the nest. They did not make as many foraging trips as did Rainy Lake males, but seemed to spend most of their time perched away from the nest site. Subjectively, much of this behavior seemed linked to female Osprey behavior. Some females appeared less tolerant of their mates perching at the nest site. Namakan Lake females were the least tolerant; perhaps an indication that these birds needed more food.

Ultimately there is a ceiling as to how much time a male will invest in foraging for any one particular brood (Poole 1982). Jamieson et al. (1982b) reported that there is an advantage in a male spending more time at the nest site in terms of territorial defense, particularly against unmated Osprey males soliciting potential mates. Jamieson et al. (1982b) also showed that males nesting farther from main foraging areas can provide their mates and

young with the same amount of food as those nesting closer, but spend significantly less time perched near their nests. This may indicate that the nests observed on Kabetogama Lake in 1986 were closer to food sources.

Although no direct relationship between foraging and fluctuating water levels was identified, water levels may affect Osprey foraging indirectly by affecting their source of food. An additional factor influencing Osprey foraging may be percentage of littoral zone. Lakes with a higher percentage of shallow water may be most beneficial to Ospreys because they provide greater foraging opportunities. Black Bay in Rainy Lake is an example of good Osprey foraging habitat. This area provides food to Kabetogama Lake birds in addition to the birds breeding in Rainy Lake. It is possible that access to this productive area may account for the higher values of reproductive success found in the Rainy and Kabetogama regions.

Subjectively, human activity did not appear to deter Osprey foraging. Ospreys were frequently observed foraging at Seegert's Marina on Frank's Bay, Rainy Lake, despite much human activity and numerous boats. They were also observed feeding along heavily developed shoreline on both Rainy and Kabetogama Lakes.

Present and Past Osprey Population Characteristics.--Using band return data Henny and Wight (1969) estimated that Ospreys in New York and New Jersey must produce 0.95-1.30 young per nest to maintain the population. Several populations reproducing within this range have been reported as stable including a Chesapeake Bay population (Reese 1977) and a population at Flathead Lake, Montana (MacCarter 1972). If these rates are applicable to the Voyageurs population, then the population is reproducing at a rate that will maintain a stable population. Nest record data from 1973-1986 indicate that the population is increasing. Reproductive and fledging success values for Ospreys in Voyageurs are intermediate between those reported for four other studies (Table 10). The Voyageurs and Chippewa National Forest populations are the most similar; reproductive success for these areas is virtually the same. However, the percentage of nests fledging young is lower at Chippewa National Forest. Population densities of Ospreys in Voyageurs and Chippewa National Forest are much lower than the more western populations, which generally exist in greater concentrations around more isolated water sources. The Voyageurs Osprey population compares favorably with other inland populations and, in fact has a higher reproductive rate than the Chippewa National Forest population (Mathisen 1972), to which it is ecologically similar. The comparison with Chippewa National Forest may be somewhat biased, however, because the Chippewa National Forest figures were generated in 1968-1971 when Voyageurs reproductive success rate may also have been lower. Also DDT and other pesticides had not yet been banned, and there is some evidence that these chemicals affected the Minnesota populations (Henny and Ogden 1969).

It was not possible to reconstruct the Osprey population that existed in the park during the pre-1900's. There are few reliable data before 1973. However, from the early 18th century through the 19th century the area that now comprises Voyageurs National Park was intensively trapped and logged

Table 10: Comparison of breeding success values of Ospreys in Voyageurs National Park, 1973-1986, with values from other Osprey populations.

Region	Occupied Nests	Number of Fledglings	Nests Fledging Young (%)	Reproductive Success (fledglings/pair)	Source
Voyageurs 1973-1986	209	202	61	0.98	This study and Grim (unpublished data)
Chippewa National Forest 1968-1971	190	156	45	0.82	Mathisen (1972)
Yellowstone National Park 1972-1977	144	105	44	0.73	Swenson (1979)
Cascade Reservoir (Idaho) 1978-1980	155	212	68	1.37	Van Daele and Van Daele (1982)
Missouri River (Montana) 1981-1982	83	93	52	1.12	Grover (1984)

suggesting that suitable Osprey habitat either was limited or not present. We cannot be certain that an Osprey population was present in the Voyageurs National Park area before the fur trade began in the mid-17th century, although it is likely that suitable habitat was abundant.

History of Beaver Ponds in Voyageurs National Park.--General knowledge of the fur trade and logging industries in northern Minnesota indicates that during the early 18th century and the entire 19th century fur bearing animals (including beaver) declined from what they were during the presettlement period (C.A. Johnston pers. comm.). This probably resulted from human encroachment (e.g. overtrapping, disease, forest fires, extensive logging). Prior to this time, the fur trade was vigorous indicating that the beaver population in the region was probably large.

In 1940 there were 47 beaver impoundments on the Kabetogama Peninsula (0.16 pond/km^2) (C.A. Johnston pers. comm.). These represented less than 1% of the Peninsula, and 67% of these were inactive. In the 1960's, the beaver population nearly doubled from the 1950's numbers, and then doubled again from the 1960's to the 1980's. There has been a slower rate of increase in beaver impoundments in the past 20 years. There are currently approximately 835 beaver impoundments on the Kabetogama Peninsula of Voyageurs National Park (2.8 ponds/km^2) (C.A. Johnston pers. comm.).

We were able to compile information on the beaver population beginning in 1940. The beaver population in the area that is now Voyageurs was very low in the 1940's. From interpretation of 1940 aerial photos it was estimated that 56% of the Kabetogama Peninsula had burned during the 1930's. This may have created favorable beaver habitat by initiating succession of aspen (Populus tremuloides) and this may have contributed to the subsequent increase in beaver density during the 1950's and 1960's. The rate of increase has declined over the past 20 years, possibly as a result of saturation of available beaver habitat, and of a decrease in aspen stands (C.A. Johnston pers. comm.). Assuming that Osprey have always preferred beaver ponds for nesting sites, it is unlikely that Voyageurs had many nesting Ospreys in the 20th century until the 1950's when the beaver population was regenerating.

Water Level Fluctuation

Results indicate a difference in water level fluctuations between two of the three regions. Water level fluctuations in Voyageurs may affect Osprey indirectly through their food supply. Flooded emergent vegetation plays an important role in the spawning and early life history of northern pike (Kallemeyn 1987a). These conditions also contribute to the reproductive success of yellow perch (Kallemeyn 1987b). There are many potential spawning areas for these species but their availability is limited by water level fluctuations. In the Namakan Reservoir only Kabetogama Lake has ample shallow, vegetated flowages conducive to northern pike and yellow perch spawning. Rainy Lake also has a relatively large amount of spawning habitat. Areas on the Namakan/Sand Point Lakes are typically small and restricted to heads of bays and inlets.

A Minnesota Department of Natural Resources report (Osborn et al. 1981) discussed the effects of the current water level regime on northern pike, the major Osprey food item in the Voyageurs lakes. According to their report, there was no relationship between spring water levels and subsequent abundance of northern pike. Northern pike abundance appeared to vary over time independently of spring water levels. Considering the apparent scarcity of suitable spawning areas except at very high water levels, a correlation had been expected.

Results of studies conducted by Kallemeyn (1987a, 1987b), differed from those of Osborn, perhaps due to sampling techniques (Kallemeyn 1987b). Kallemeyn reported that suitable conditions for northern pike and yellow perch spawning only occur in Namakan Reservoir when lake levels actually

exceed the maximum levels allowed by the current water management program. Northern pike reproduction was higher when this occurred. He further indicated that correlations between yellow perch reproduction, the second most important Osprey food item, and lake levels were strongly positive. This relationship was significant only in Sand Point Lake (Kallemeyn 1987b). From Kallemeyn's study it appears that two important fish species in the Osprey diet are adversely affected by the current water level regime of the Voyageurs National Park lakes. Similar results also occurred for walleye (Chevalier 1977 and Kallemeyn 1987b), but this species was not positively identified in the Osprey diet. All of these species spawn in early May about two weeks after ice-out. Kallemeyn has suggested an alternative water level regime that may enhance their reproductive success by providing higher lake levels earlier in the spring. Based on Kallemeyn's results, water levels may indirectly affect the rate and extent of a potential Osprey population increase by limiting their food supply.

Although water level fluctuations may suppress fish species that are important components of the Osprey diet, reproductive success of Osprey does not appear linked to water level fluctuations. Reproductive success in Kabetogama was similar to Rainy and was subject to the same water level fluctuations as Namakan/Sand Point Lakes. However, similarity in reproductive success could be related to some overlap in foraging between the two regions. Kabetogama birds appear to forage in Rainy Lake and it is also possible that Rainy Lake birds forage in Kabetogama Lake. This overlap made it difficult to distinguish regional differences due to water level fluctuations.

Lake Productivity

In considering lake productivity the following factors are important: the diversity, abundance, distribution, age-structure, and behavioral characteristics of fish as well as littoral percentage of lakes. Although fish species diversity did not differ greatly among regions, abundance and biomass of some fish species did vary regionally over time (1973-1986). Throughout these years Kabetogama Lake had the greatest abundance of four of the most frequently occurring fish species in the Park, and was notable in its abundance of walleye. Sand Point Lake was notable for its population of cisco. Namakan Lake had the second greatest abundance of cisco. Rainy Lake had the greatest abundance of northern pike. Yellow perch were most abundant in Rainy and Kabetogama Lakes. In addition, Kabetogama experienced the highest human fishing pressure (Kallemeyn 1985). As a consequence more fish that were injured by fishermen as they were being released, and dead fish may have been available to Ospreys as prey items in this lake.

Distribution and behavioral characteristics of fish are probably major factors affecting Osprey breeding biology because Voyageurs Ospreys are selective and forage primarily in shallow water areas. Age-structure is also an important productivity factor to consider because only at certain ages will various fish be available to Osprey due to their size.

The amount of littoral zone is an important variable influencing Osprey feeding behavior and foraging success because Ospreys appear to prefer foraging in shallow water.. Results comparing littoral percentages among regions indicated that the Rainy Lake region has the largest littoral percentage. Much of this area is concentrated in Black Bay. Littoral areas of each of the other lakes are less than half that of Rainy Lake, and are nowhere concentrated to the extent of Black Bay. Black Bay was a site of considerable foraging activity during this study.

Differences in reproductive success may be linked to lake productivity. Namakan/Sand Point Lakes had lower abundance of northern pike and yellow perch than the other regions and also had the lowest Osprey reproductive success. Both species were important Osprey prey items. Conceivably, Ospreys compensate by utilizing species other than northern pike and yellow perch in this region. We did not have the data to test this hypothesis.

Human Disturbance

Osprey nests were originally assigned human disturbance values based on the level of human usage of the region. Kabetogama Lake was characterized as having high usage, and Namakan/Sand Point Lakes and Rainy Lakes low. Although human usage of lakes was substantial, we discovered that with only two exceptions, disturbance at nest sites was low; generally it was in the form of motorboat noise or planes overhead.

Human disturbance is generally not a problem in Voyageurs because most Osprey nests are isolated. Nor does it appear to adversely affect foraging Ospreys; individuals were frequently observed to dive within several meters of boats. In addition, birds may actually benefit from fish which have been injured by fishermen. However, if a boat approaches too closely when they are perched along the shoreline, the birds will fly.

Osprey are most sensitive to disturbances at the nest. Females on nests with eggs or young become obviously upset by humans entering the nest site area. There is variation in how close different individuals will tolerate a human intruder (50-100 m on average, although some are even less tolerant). It is important to note that there is a tendency for birds at more remote nests to be less tolerant of humans. Human disturbance that results in adults leaving the nest is potentially more detrimental during incubation and early hatching than in later stages of the reproductive cycle. During incubation, eggs may be exposed to low or high temperatures for an extended period of time; high temperatures are potentially more detrimental. Disturbance during rain or high winds may be very harmful to young Osprey that are not yet homeothermic.

Ospreys seem able to habituate to human disturbance to some extent. Levenson and Koplin (1984) compared three groups of Osprey nests: (1) no disturbance or minimal disturbance, (2) relatively constant disturbance, probably present even before nesting began, and (3) no initial activity during incubation followed by intense activity mid-incubation through end of nesting season. They found the percent of occupied nests producing

fledglings and reproductive success declined with increasing activity levels (1-3). They concluded that a substantial increase in human activity has a significant adverse effect on productivity after Ospreys begin nesting. It seems likely that Wood Duck Island is a Type 3 nest. When the pair initially occupies the nest and begins incubation in early May there is little human disturbance. In mid-May when fishing season opens the birds are approximately midway through incubation, and there is an influx of human activity near the nest. Despite these circumstances there has been a nest on Wood Duck Island and/or Zollner Island (the Grassy Islands) since 1976. Both have been successful six out of ten years and have produced 11 chicks. The same adults (and possibly their progeny) may have used these sites in consecutive years (Newton 1980). These birds have probably become habituated to the disturbance patterns near these sites indicating that Osprey are somewhat flexible in regard to human disturbance. Regardless, even these birds become alarmed when people approach their nest too closely, indicating that no form of human activity on these islands should be permitted at any stage of the breeding cycle.

Because it was low in all regions, human disturbance also does not conclusively explain the lower reproductive success measured in the Namakan/Sand Point region.

CONCLUSIONS

There are currently (1985-1986) 24 Osprey nests in Voyageurs National Park, indicating an adult population of at least 48 birds; based on trends from the 1973-1986 data, this population is increasing. The general Osprey nest site distribution in Voyageurs can be considered clumped with three areas of nest concentrations in the Park: (1) several large bays off Grassy Bay in Sand Point Lake, (2) east Kabetogama, (3) west Kabetogama extending into Black Bay in Rainy Lake.

In 1985 and 1986, mean reproductive success for Voyageurs National Park was 1.04 fledglings per occupied nest with no regional differences. While there was some variation in the other reproductive characteristics, the only regional differences were in the number of nestlings and percentage of nests fledging young. In both cases these differences were between the Rainy and Namakan/Sand Point regions. The number of occupied nests per region has increased since 1973. There has been a similar increase in number of fledglings in all regions except Namakan/Sand Point. Reproductive success has increased over the years 1973-1986 in the Kabetogama region only. It has varied inter-annually from 0-2 fledglings/pair, and averaged 0.98 fledglings/pair for the Park as a whole over these years. Reproductive and fledging success data on the Voyageurs Ospreys are intermediate between those reported in other studies. Based on estimates determined by Henny and Wight (1969) it is a stable population.

Assuming that Ospreys have always preferred beaver ponds for nesting sites, it is unlikely that the area which is now Voyageurs National Park had many nesting Ospreys between the mid-18th century and the early 1900's while the beaver population was being heavily exploited. In addition, extensive

logging during this period would have eliminated most alternative Osprey nesting sites. A regeneration of the beaver population began in 1940. This coincided with reduction in beaver exploitation coupled with creation of favorable beaver habitat by succession of aspen (Populus tremuloides). Currently the Osprey population does not appear limited by nest site availability.

The only difference that we detected in foraging behavior among regions was that birds in the Rainy Lake area of Voyageurs National Park tend to deliver a greater number of fish/hour to the nest. Foraging behavior among individual Ospreys was highly variable.

The average annual water level fluctuation in Rainy Lake is 1.0 m while in the Namakan Reservoir (including Kabetogama, Namakan, and Sand Point Lakes) it is 2.7 m. The pattern of these fluctuations differs from that of the natural fluctuations, and simulates flood and drought conditions.

In 1985-1986 Kabetogama Lake was the most productive lake in terms of CPUE of fish in experimental gill nets (both numbers and weights of fishes). Sand Point Lake generally ranked second, Namakan third, and Rainy Lake had the overall lowest catch per unit effort. Rainy Lake, however, had the greatest and most concentrated littoral percentage and the highest catch per unit of effort of northern pike, the Ospreys preferred prey.

Human disturbance was low at most Osprey nest sites; it consisted primarily of motorboat noise and low flying private aircraft. Osprey response to human disturbance generally consisted of (1) looking at the source of disturbance or, (2) no response. Disturbances adversely affect Osprey if they occur within 50-100 m of the nest.

Based on the results of the stochastic model, it appears that the Osprey population in Voyageurs can tolerate a certain amount of human disturbance (human activity within 1 km of the nest). However, based on our observations, if human disturbance increases adjacent to nests (50 -100 m), Osprey reproductive success will probably decline.

There is no evidence that Osprey abundance, distribution and reproductive success are influenced directly by differences in water level fluctuation, lake productivity or human disturbance among regions. However, because water level fluctuations may suppress populations of fish species that are important components of Osprey diet, water levels may indirectly influence nest site distribution and foraging behavior. Whether or not water levels affect reproductive success, and ultimately Osprey population dynamics in Voyageurs National Park, is difficult to determine. Ospreys appear to compensate for regional differences in availability of fish by traveling the distance needed to secure food for their offspring. In a food stressed population regional differences in reproductive success might be more pronounced. The most important factors that currently appear to be influencing Osprey numbers in the Park are: (1) a large beaver population that creates new nest trees through pond construction, (2) large and diverse populations of fish throughout the Park, and (3) minimal human disturbance.

RECOMMENDATIONS

- (1) Voyageurs National Park staff should continue their excellent long term aerial monitoring program that annually estimates Osprey distribution, abundance and reproductive success.
- (2) The location of important Osprey foraging areas should be recorded for future management considerations.
- (3) Human activity should not be allowed within 50-100 m of an Osprey nest. This includes boats (motorized and unmotorized), aircraft, and persons on foot. In addition, neither trails nor campsites should be constructed within this distance.
- (4) An Osprey dietary study should be conducted to determine more precisely the proportions of fish species consumed and how prey species composition varies among regions, particularly in preferred foraging areas.
- (5) A long term study on Osprey occupation of beaver ponds should be initiated to determine the phenology of the Osprey/beaver relationship from initial formation of ponds through disappearance of suitable nest trees.

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