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Reproductive ecology of ospreys (Pandion haliaetus) in the Bitterroot Valley of western Montana

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REPRODUCTIVE ECOLOGY OF OSPREYS (*Pandion haliaetus*) IN THE BITTERROOT VALLEY OF WESTERN MONTANA

by

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ABSTRACT

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The population status and reproductive success of ospreys in the Bitterroot Valley of western Montana were studied during the 1983 and 1984 breeding seasons. These ospreys reproduced at a rate of 1.89 fledglings per active nest per year, a rate well above that (0.79-1.30) required for replacement, as calculated for other populations. Reproductive success did not differ for the 2 years of the study, and was not limited by food availability or human disturbance. Nest site characteristics were measured for the population and differed between pond and river habitats in the study area, though no differences in young fledged per active nest were found between habitats. More young fledged per successful pond nest than river nest in 1984 though reasons for this were not found.

Growth of the population is similar to that of other populations in the western United States, and is probably a result of the discontinued use of DDT and the recent formation of reservoirs in these areas. Suitable nest trees appear to be present throughout much of the study area, although the possibility exists that nest sites may become limiting in the future.

ACKNOWLEDGMENTS

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INTRODUCTION

The osprey (Pandion haliaetus) is a medium-sized hawk of the family Accipitridae. Scattered populations of breeding ospreys occur world-wide, with populations from temperate zones migrating to tropical and subtropical localities during the fall and winter months. Non-migratory osprey populations remain in subtropical areas throughout the year (Friedman et al. 1950, Brown and Amadon 1968, Ogden 1975, 1977).

Osprey reproduction has been studied in much of its range since the early 1960s, when large scale population declines were documented along the eastern seaboard of the United States (Emerson and Davenport 1963, Ames and Mersereau 1964, Peterson 1969) and in certain areas of California (Diamond 1969). The primary cause of the drastic population declines was reduced hatching success induced by concentrations of organo-chlorine residues in the tissues and eggs (Ames and Mersereau 1964, Weimeyer et al. 1975, Spitzer et al. 1977).

Other factors known to limit reproductive success in birds of prey are limited habitat, limited food resources, predation, human disturbance, and inclement weather. Data on these factors indicate that they can have a negative influence on osprey productivity, but do not induce large scale population declines (Koplin et al. 1972, Swenson 1979, Poole 1981, Van Daele and Van Daele 1982).

Data on the population dynamics of inland and Western ospreys prior to the late 1960s are relatively scarce, although large populations were known to have inhabited areas of central and southern California and northwestern Mexico (Diamond 1969:60). Only remnants of these historical populations exist today (Henny 1983). Recent data, however, indicate that many inland populations of ospreys are expanding their present range, apparently because of the formation of reservoirs along inland river systems (Van Daele et al. 1980, Swenson 1981a, Henny 1983, Grover 1984). The population base from which expansions are taking place is not always known. The possibility that some of these expansions are in response to the discontinued use of DDT, as has been shown for some East Coast populations (Spitzer and Poole 1980), cannot be discounted (Johnson et al. 1975, MacCarter and MacCarter 1979) and may, in fact, be ascertainable once the population dynamics of a particular population are known. By comparing parameters of reproduction and time-activity budgets of expanding populations with those of previously studied ones, determining the extent to which each factor is affecting currently growing osprey populations may be possible.

I chose the Bitterroot Valley as a study area because it had a healthy, expanding osprey population that had not been intensively studied, a history of fairly intense pesticide use (Ron Escano, pers. commun.), and 2 distinct habitat types (pond and river) between which comparisons could be made. Other areas in and around western Montana, including Flathead Lake (MacCarter and MacCarter 1979, Klaver et al. 1982), western Idaho (Van Daele and Van Daele 1982), the Missouri River headwaters (Grover 1984) and Yellowstone National Park (Swenson 1979), have been intensively studied. Thus, the opportunity existed to compare reproductive rates recorded during those studies with those found in the Bitterroot Valley. The primary objectives were to:

1. document population status and reproductive success of Bitterroot ospreys; and

2. assess the effects of habitat, human disturbance, predation, and inclement weather on the reproductive success of this population.

STUDY AREA

The Bitterroot Valley is a 770 square km valley situated directly south of Missoula in west-central Montana. The valley is 75 km long from north to south, and averages 11 km wide from east to west. It is bounded on the east by the Sapphire Mountains and on the west by the Bitterroot Range. The Bitterroot River runs from south to north through the Valley from its origin, 3 km south of Darby, to its confluence with the Clark Fork River, 8 km west of Missoula (McMurtry et al. 1972, Fig. 1).

The study site lies along the Bitterroot River (River) between Corvallis and Lolo, Montana. Included within this area are roughly 40 km of river and 200 ha of water impoundments on the Lee Metcalf National Wildlife Refuge (Refuge). The 1120-ha Refuge is situated adjacent to the River 2 km north of Stevensville (Fig. 2).

The Refuge was authorized as the Ravalli National Wildlife Refuge by the Migratory Bird Conservation Commission in December 1963 (Flath 1970) for the management of breeding waterfowl populations. The flooding of timbered lands on the Refuge, as the impoundments were forming, resulted in large numbers of dead and dying trees in and around many of the impoundments. U.S. Fish and Wildlife personnel placed 38 Canada goose (*Branta canadensis*) nesting structures on the Refuge impoundments (Flath 1970). Many of those snags and goose nesting structures have since become bases for osprey nests, which are used by both geese and ospreys each year.

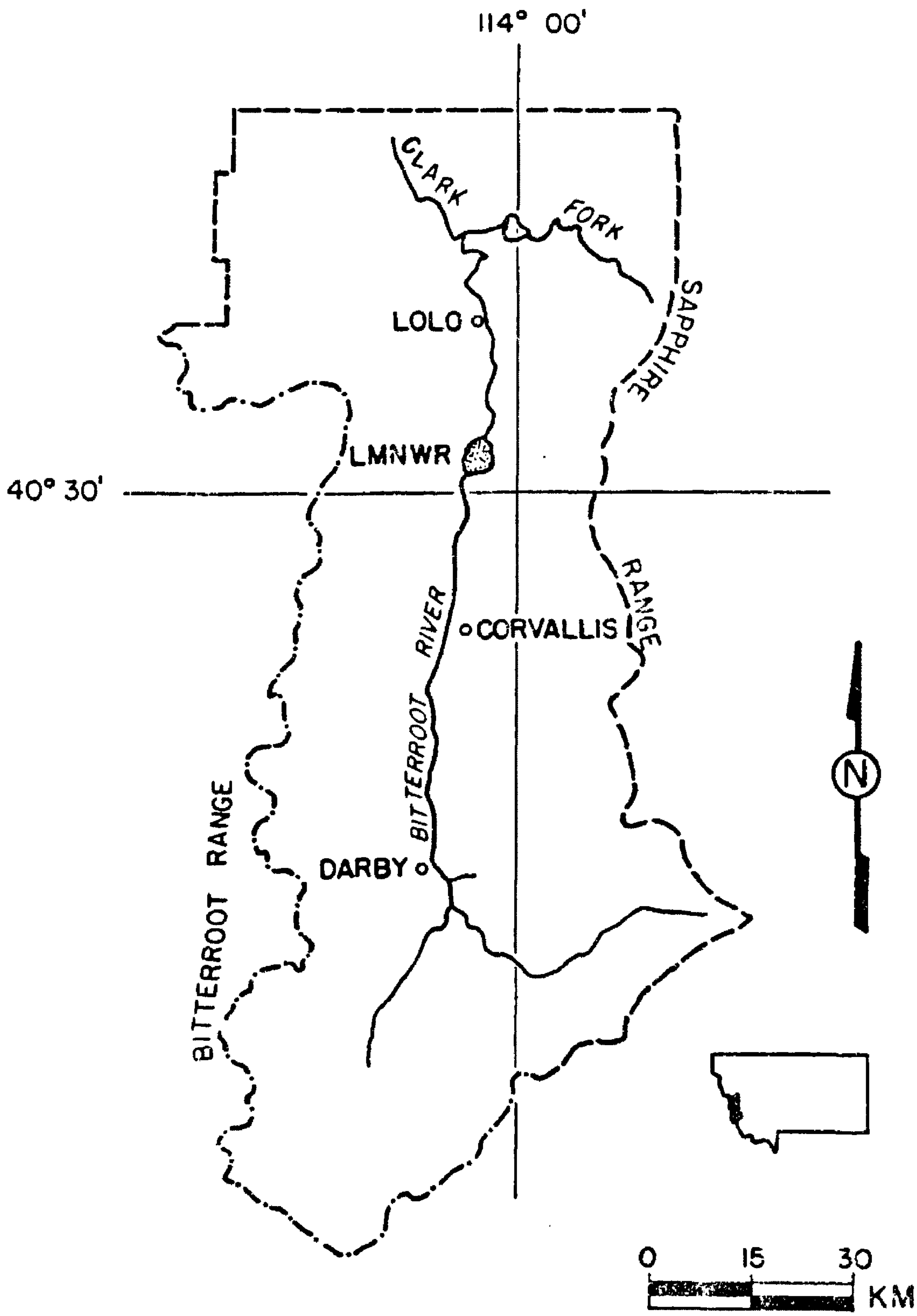

Figure 1. Map of the Bitterroot Valley. The Bitterroot River flows north from Darby to Missoula.

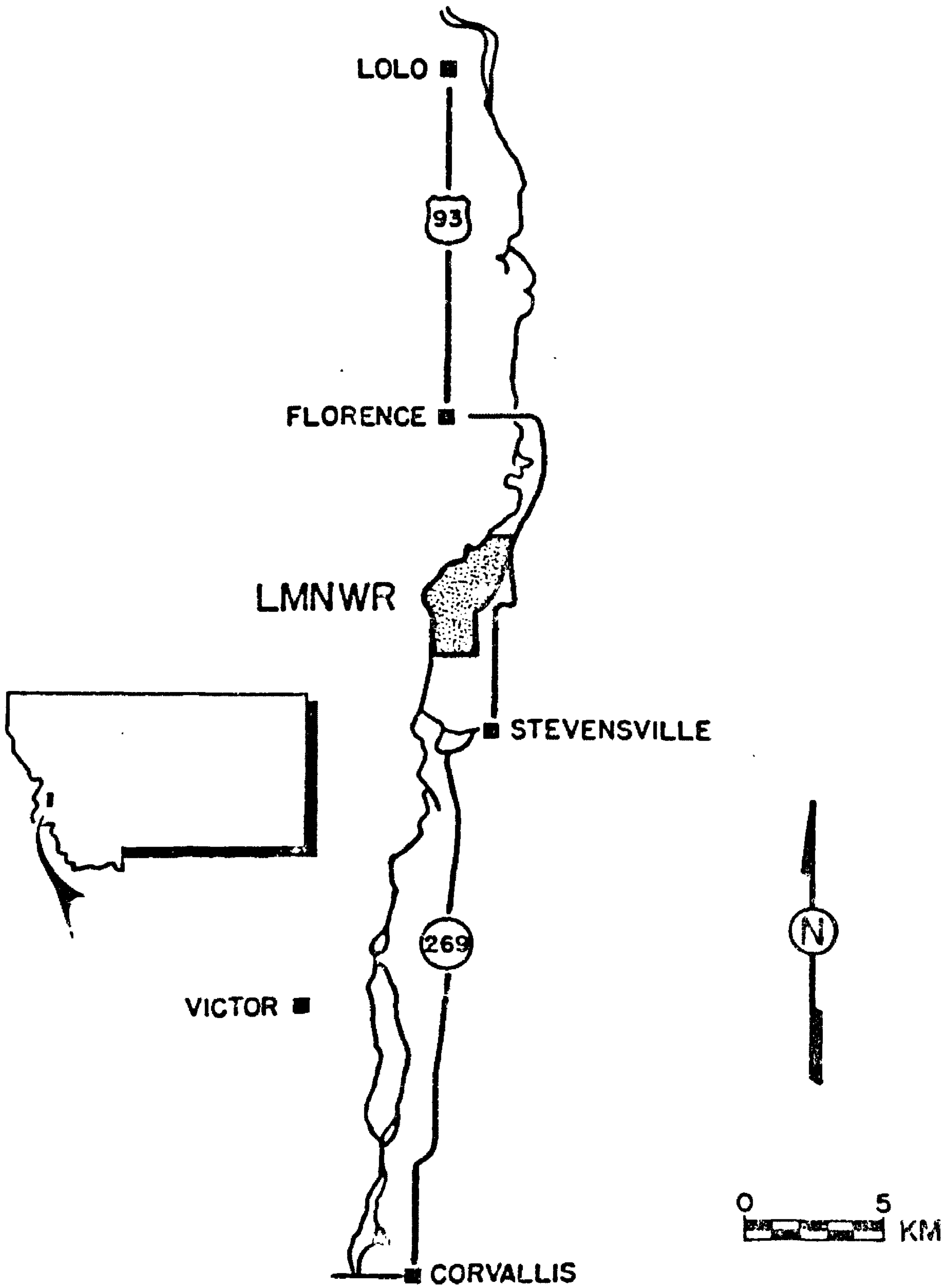

Figure 2. Map of the Study Area between Corvallis and Lolo, including the Lee Metcalf National Wildlife Refuge 2 km north of Stevensville.

Habitat along the Bitterroot River is characterized by dense growth of trees and brush interspersed with open meadows and pastures. Dominant trees of forested areas are black cottonwood (_Populus trichocarpa_) and ponderosa pine (_Pinus ponderosa_). Snags are formed along the River primarily as a result of tops broken during wind storms.

Much of the bottomland along the River is in private ownership, thereby restricting human access to either foot travel along the bank or boat travel on the River itself. Boating and fishing are major activities on the River during the spring and summer, bringing ospreys and humans into frequent contact. Approximately 90% of the osprey nesting areas on the Refuge, and all of the pond nests are inaccessible to humans during the osprey breeding season.

METHODS

Nest location surveys were initiated in February 1983, with myself and 1 observer floating the Bitterroot River in a 17 ft. Coleman canoe. Two days were used to float the River and locate nests between Tucker Crossing and Florence Bridge (Fig. 2). A fixed-wing aircraft flight took place in mid-March 1983 to check for nests in previously floated areas and to locate nests in the Corvallis-Tucker and Florence Bridge-Lolo sections of the River. Foot travel along the River throughout the study area in April enabled me to identify new nest sites, verify nest locations, and record approximate dates when ospreys returned. During mid-April 1984, a fixed-wing aircraft flight took place to check for remaining 1983 nests and to locate new 1984 nest sites. Nest site locations were recorded and later located on U.S.F.S. National Forest Maps. Refuge nests were located by automobile and foot travel on the Refuge grounds during both years and were recorded on a Refuge map. As the breeding seasons commenced, nests were classified after Postupalsky (1974) as occupied, active, successful, or alternate. Nests where at least 1 bird was present through the pre-incubation period were classified as occupied. Of the occupied nests, active nests were those at which 1 or more eggs were laid, and nests that produced at least 1 fledgling were defined as successful. Alternate nests were unoccupied nests within the nesting territories that were used in any way by nesting ospreys.

Data on time and numbers of eggs laid, nestlings, and fledglings for each nest were gathered by foot travel and fixed-wing aircraft flights during mid-May, late June and mid-July, and late July and early August for each breeding season. These results were tabulated for each nest, habitat type, and the population for each breeding season. These data are available by individual nest for 1984 only because of a house fire that destroyed specific nest site data for 1983. Statistical comparisons of reproductive success between habitat types in 1984 were carried out using the SPSSX program on the University of Montana Dec 20 computer. Due to loss of the 1983 raw data, comparisons between 1983 and 1984 reproduction are limited to comparison of means for the 2 years, with the assumption of equal variances around each year's means. Ninety-five percent confidence intervals for the 1984 means were calculated using SPSSX.

To document the division of labor between male and female ospreys and energy spent in potentially important breeding activities in the 2 different habitats, I recorded time-activity budgets, food delivery rates, prey species composition, and general breeding behavior for the population. Data for these parameters were gathered by direct continual observation during 4-16 hour periods, 16-40 hours per week, for both breeding seasons. One River and 4 pond nests were observed in 1983 from pre-incubation to time of fledging, and 3 pond and 2 river nests were observed from incubation through post-fledgeing in 1984. Secondary sex characteristics (MacNamara 1977) and observed individual behavioral traits were used to determine sex of individual ospreys. Behaviors recorded during direct observations for time-activity budgets are shown in Table 1. Times ospreys were engaged in various activities were recorded to the nearest minute from the beginning to the end of an activity. Time spent fishing, when not in sight, was determined from when a bird left the area and returned with a fish. When ospreys returned with a partially-eaten fish, time spent fishing was recorded as one half of time spent out of sight and the other half was recorded as feeding time. Species and lengths (relative to osprey body size) of fish delivered to nests were assessed during observation periods. Fish lengths were grouped into categories of 6-8, 8-10, 10-12, and 12-14 inches, and were later converted to metric lengths. Grams of fish delivered was calculated using a length-mass relationship formula: Log (Mass(g)) = .0359(Length(cm)) + 1.45, derived from data in Carlander (1915).

Nest site characteristics of 10 pond and 15 river nests were assessed during the study. Tree height, nest height, DBH, tree condition, distance to water, dominance ranking of tree in stand (1 = open - 5 =totally surrounded), and species of tree were recorded and tabulated to assess average characteristics of osprey nest sites for the study area. Tree and nest heights were measured using a standard 100-foot cloth tape and a clinometer. Distance to water (where applicable) was measured using the same 100-foot tape. DBH was measured using a U.S.F.S. "D" tape. Measurments were converted to metric form for presentation. Future nest site potential, and human disturbance potential were assessed for each nest site.

Table 1. Time-activity budget parameters recorded during direct, continual observation periods.

1.	Perching
2.	Feeding
3.	Courtship flight
4.	Aggressive flight
5.	Actively fishing
6.	Gathering nest materials
7.	Nest maintenance
8.	Mounting
9.	Copulating
10.	On nest (Incubating)
11.	Unknown

RESULTS

A total of 49 nests were occupied by ospreys during the study. Nest surveys prior to and at the onset of the breeding season were very successful in locating osprey nests, and I am confident that all of the occupied nests in the area were located before egg laying occurred. Nesting territories were distributed throughout the study area, with groups of nests occurring sporadically along the river bottom (Fig. 3).

Breeding Season

Ospreys began arriving on the study area on 1 April during both breeding seasons. New arrivals occurred daily until 25 April in 1983, and 1 May in 1984, when all ospreys were present in the area. At nests where the sex of the first returning bird could be determined, males and females returned with approximately equal frequency. Time between arrivals at a nest varied from 0 to 7 days.

Nest construction began from 0 to 2 days after a first bird returned and continued throughout the pre-incubation period (Fig. 4). Both adults supplied sticks, twigs, and grasses for the construction or repair of a nest. Days required for nest construction varied with condition of nests upon return. Some nests needed only minor repairs while others had to be completely built. In 1984, initiation of nest construction was delayed for approximately half of the osprey pairs because of Canada Geese nesting in osprey nests. Some ospreys built new

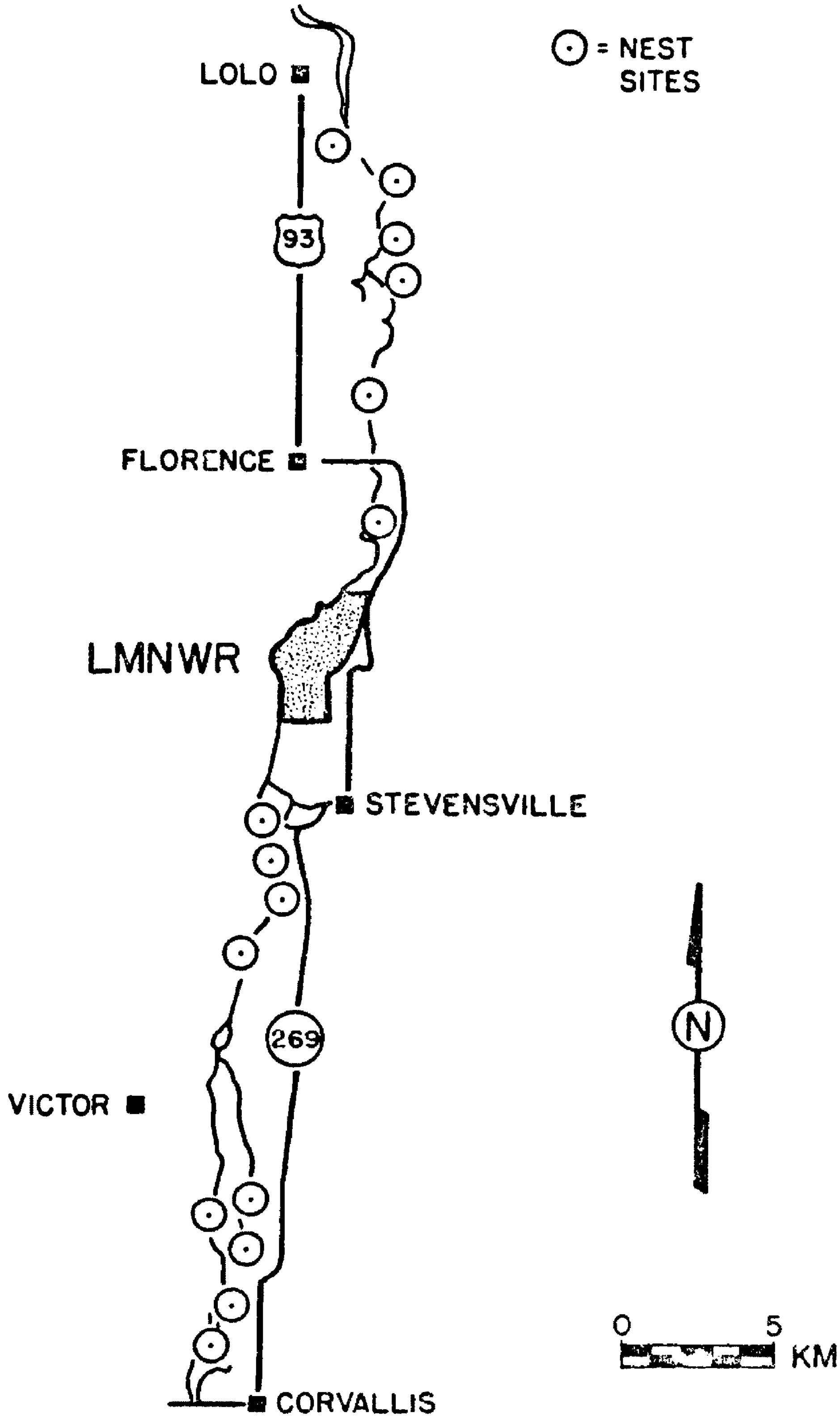

Figure 3. Distribution of osprey nesting sites on the river portion of the study area.

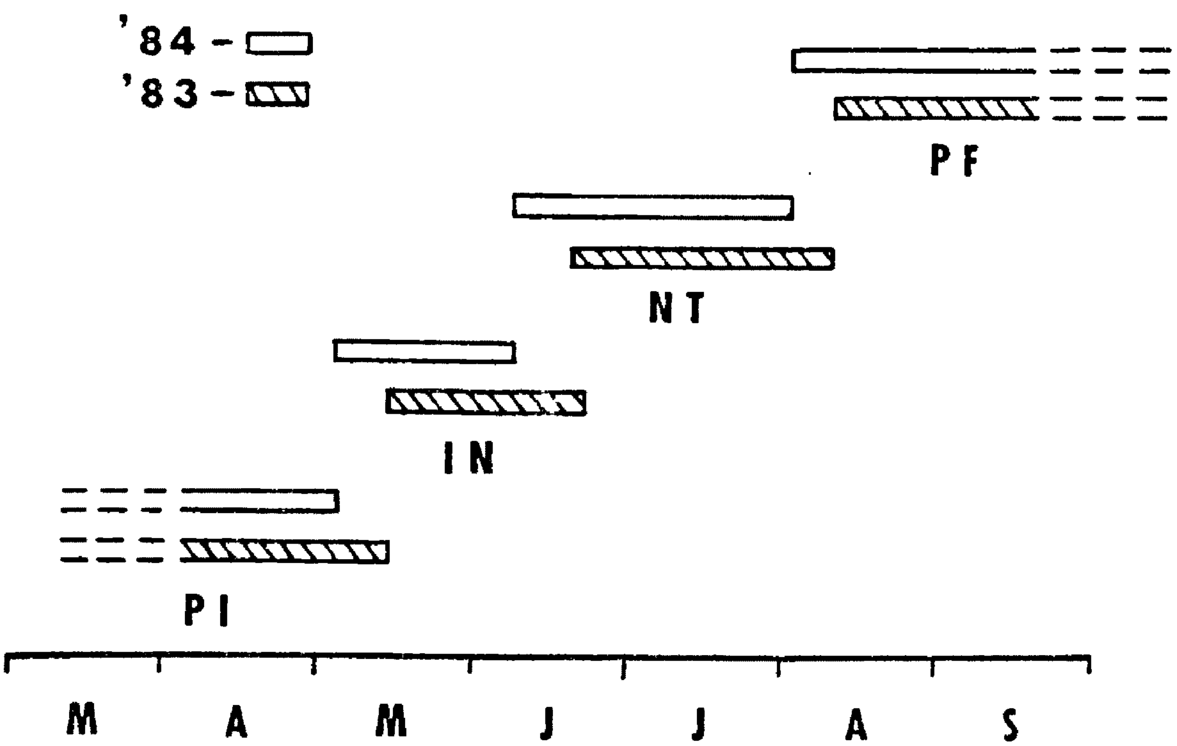

Figure 4. Breeding season chronology for Bitterroot ospreys, 1983-1984. PI = Pre-incubation phase, IN = Incubation phase, NT = Nestling phase, PF = Post-fledging phase. Bars indicate time period of each breeding phase.

nests on trees adjacent to their "desired" goose-occupied nests, during which time they were seen harrassing the nesting geese.

Courtship displays by males directed toward females occurred periodically. These displays consisted of males flying, hovering, and swooping, with sticks, fish, or nothing in their talons, chirping throughout the performance (Fig. 5). The number of copulations/day increased significantly from arrival to egg laying (chi-squared = 8.6, $p < .005$) during the 1983 pre-incubation period (Fig. 6).

The incubation period for ospreys begins when the first egg is laid. Eggs are laid and subsequently hatch asynchronously, with a 1-3 day period between the laying of each egg (Poole 1981). The incubation period began in the Bitterroot between 8 and 13 May in 1983 and 2 and 9 May in 1984. Incubation lasted between 30 and 35 days for both breeding seasons (Fig. 4). Both sexes incubated at all observed nests during this study, though females were responsible for about 70% of all time spent incubating (see time-budget analysis for detailed description).

The nestling period began in the Bitterroot between 15 and 20 June in 1983 and 2 and 10 June in 1984 with the hatching of the eggs. The nestling period for this population was between 55 and 60 days (Fig. 4) for both seasons, and ended with the fledging of the young in mid-August in 1983 and late July-early August in 1984. During the post-fledging period, fledglings gradually increased their flying skills and eventually, along with the adults, left the valley by mid- to late September.

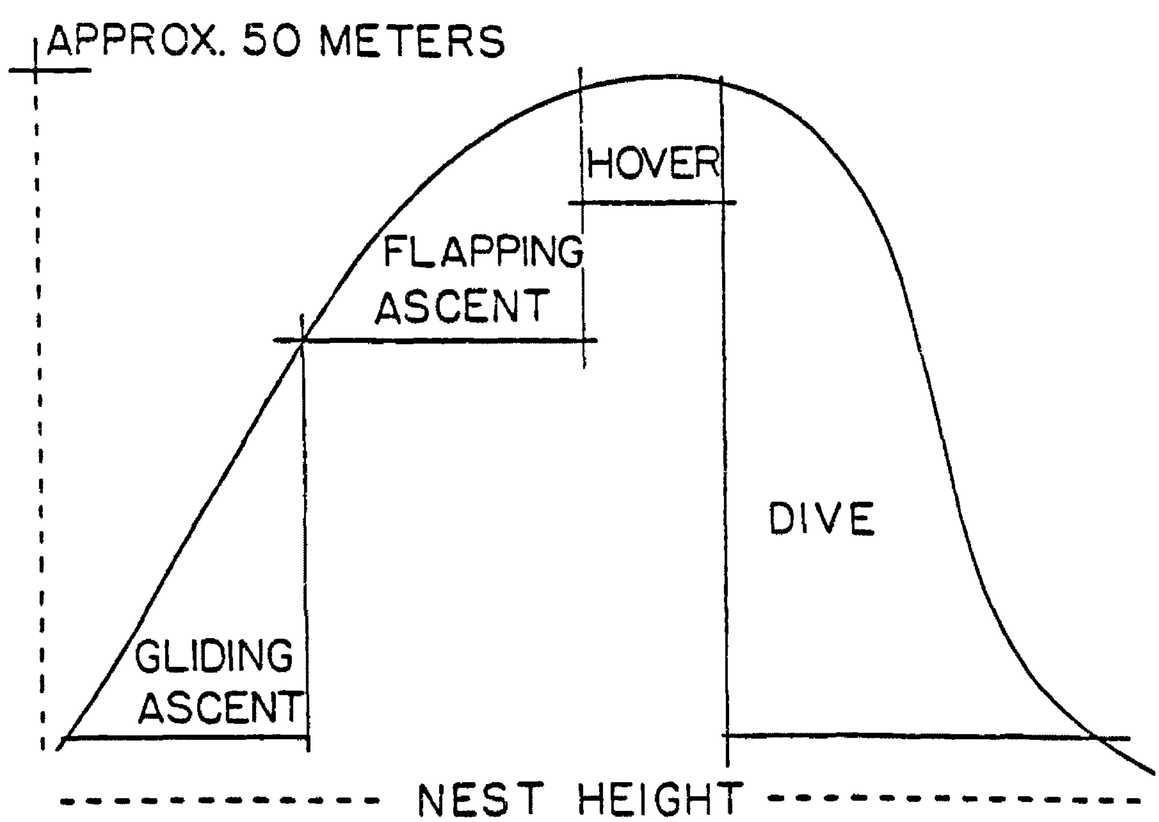

Figure 5. Pattern of male osprey courtship flight.

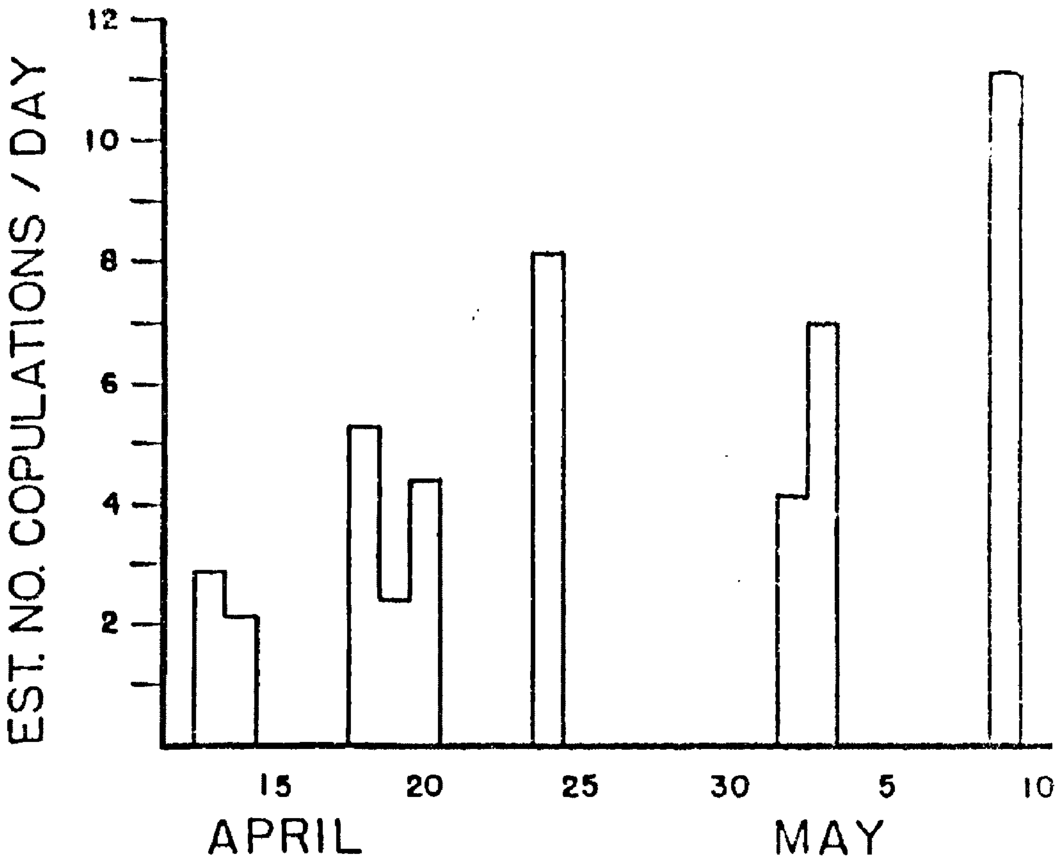

Figure 6. Estimated number of copulations/day during pre-incubation, 1983.

Reproductive Success

The number of occupied nests in the study area increased from 22 in 1983 to 27 in 1984, with increases occurring in both habitats (Table 2). The number of active nests, however, increased by only 1, from 18 to 19, and resulted from a reduction, from 10 to 8, in the number of active river nests, and an increase, from 8 to 11, in the number of active pond nests. The ratio of successful/active nests in each habitat remained consistent during the 2 years. As shown in Table 2, once active, 17 of 18 river nests and 14 of 19 pond nests were successful.

Greater percentages of eggs hatched in river nests (77.8, 95.0) than pond nests (71.4, 90.3) during the 2 seasons (Table 3), though these differences were not statistically significant ($P > .05$). The hatching rate (number hatched/laid) for the 1983 population was significantly lower (t-test, $P < .05$) than that in 1984, though fledging rates (number fledged/hatched) did not differ significantly between the 2 years.

Productivity, as measured by the number of young fledged/active nest, increased slightly from 1983 to 1984 in both habitats, and was similar between habitats each year (Table 4). Brood size (number fledged/successful nest) in 1984 was greater, though not significantly so, than in 1983 ($P > 0.05$), while brood size in pond nests in 1984 was significantly greater (t-test, $P < .05$) than that in river nests. Brood size, when compared with number fledged/active nest is an indicator of the number of active nests lost in a population.

Table 2. Activity and distribution of osprey nests in the Bitterroot Valley, 1983-1984.

	River		Pond		Total	
	'83	'84	'83	'84	'83	'84
Occupied	11	14	11	13	22	27
Active	10	8	8	11	18	19
Successful	9	8	6	8	15	16

Table 3. Hatching and fledging success of Bitterroot Ospreys, 1983-1984.

	No. Eggs laid	No. Hatched	(%H/L)	No. Fledged	(%F/H)	(%F/L)
RIVER						
1983 -	27	21	(77.8)	18	(85.7)	(66.7)
1984 -	20	19	(95.0)	16	(84.2)	(80.0)
total -	47	40	(85.1)	34	(85.0)	(72.3)
POND						
1983 -	21	15	(71.4)	13	(86.7)	(61.9)
1984 -	31	28	(90.3)	23	(82.1)	(74.2)
total -	52	43	(82.7)	36	(83.7)	(69.2)
COMBINED						
1983 -	48	36	(75.0)	31	(86.1)	(64.6)
1984 -	51	47	(92.2)	39	(83.0)	(76.5)
total -	99	83	(83.8)	70	(84.3)	(70.7)

H = hatched, L = laid, F = fledged

Table 4. Reproductive success of Bitterroot Ospreys, 1983-1984.

	Pond(N)	River(N)	Total(N)
Eggs/active			
1983 -	2.65(8)	2.70(10)	2.67(18)
1984 -	2.82(11)	2.50(8)	2.68(19)
total -	2.75(19)	2.61(18)	2.68(37)
Young/active			
1983 -	1.88(8)	2.10(10)	2.00(18)
1984 -	2.55(11)	2.38(8)	2.47(19)
total -	2.26(19)	2.22(18)	2.24(37)
Fledge/active			
1983 -	1.63(8)	1.80(10)	1.72(18)
1984 -	2.09(11)	2.00(8)	2.05(19)
total -	1.89(19)	1.89(18)	1.89(37)
Fledge/successful			
1983 -	2.16(6)	2.02(9)	2.07(15)
1984 -	2.88(8)	2.00(8)	2.44(16)
total -	2.57(14)	2.00(17)	2.26(31)

A total of 6 nest failures were recorded during the study, 5 of which were pond nests (Table 2). Three of the 5 pond failures were caused by high winds, which either blew nests out of trees or blew nest trees over. Causes for the 3 remaining failures have not been determined, and may be due to predation, because no remains of eggs or young were seen in these nests after they had failed. The relatively large number of pond nests destroyed by wind indicates a higher susceptibility to wind of pond nests, and may be due either to the relative openness of pond nests as compared to river nests (see nest site characteristics, Table 9), or the flooded condition of nest trees on the refuge ponds (see study site description).

Time-activity Budgets

During this study, both male and female ospreys spent the majority of their daylight hours in non-flying activities. Males spent between 70 and 80% of their time perching, feeding, and incubating throughout each breeding season, 10 and 15% fishing or gathering nest material, and 10-25% in unknown activities (Table 5, Fig. 7). Females were inactive for 85-90% of their time and nest building and unknown activities took 3-5% and 5-10% of their time, respectively (Table 5).

Table 5. Approximate percent of daylight time ospreys engaged in activities during pre-incubation to fledging, 1983, and, incubation to post-fledging, 1984.

	1983						1984						Combined							
	PI		IN		NT		IN		NT		PF		PI		IN		NT		PF	
Activity	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Perching	30	20	40	20	45	17	38	14	50	20	50	20	30	20	39	19	48	19	50	26
Feeding	7	10	7	5	22	11	5	5	10	15	10	11	7	10	6	5	17	12	10	11
Courtship Flight	<1	0	0	0	0	0	<1	0	0	0	0	0	<1	0	0	0	0	0	0	0
Aggressive Flight	<1	0	<1	<1	<1	<1	1	<1	<1	<1	<1	<1	<1	0	<1	<1	<1	<1	<1	<1
Fishing	7	0	5	0	12	0	5	0	7	0	12	0	7	0	5	0	11	0	12	0
Obtaining Nest Material	6	3	1	<1	1	2	2	2	<1	<1	2	2	6	3	2	1	1	1	2	2
Nest Maintenance	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1
Mounting	<1	<1	0	0	0	0	0	0	0	0	0	0	<1	<1	0	0	0	0	0	0
Copulating	<1	<1	0	0	0	0	0	0	0	0	0	0	<1	<1	0	0	0	0	0	0
On Nest	30	60	33	70	5	65	34	73	13	57	5	45	30	60	34	70	4	63	6	45
Unknown	18	6	13	5	15	5	14	5	29	7	21	15	18	6	13	5	17	4	21	15
Flying	14	3	6	1	13	2	9	3	8	1	15	3	14	3	8	2	13	2	15	3
Non-Flying	67	90	80	95	72	93	76	92	63	92	65	82	67	90	79	94	70	94	65	82

1983 Hours Observed: PI = 180, IN = 120, NT = 150

1984 Hours Observed: IN = 80, NT = 95, PF = 50

M = Male, F = Female; PI = Pre-Incubation, NT = Nestling, PF = Post-Fledgling

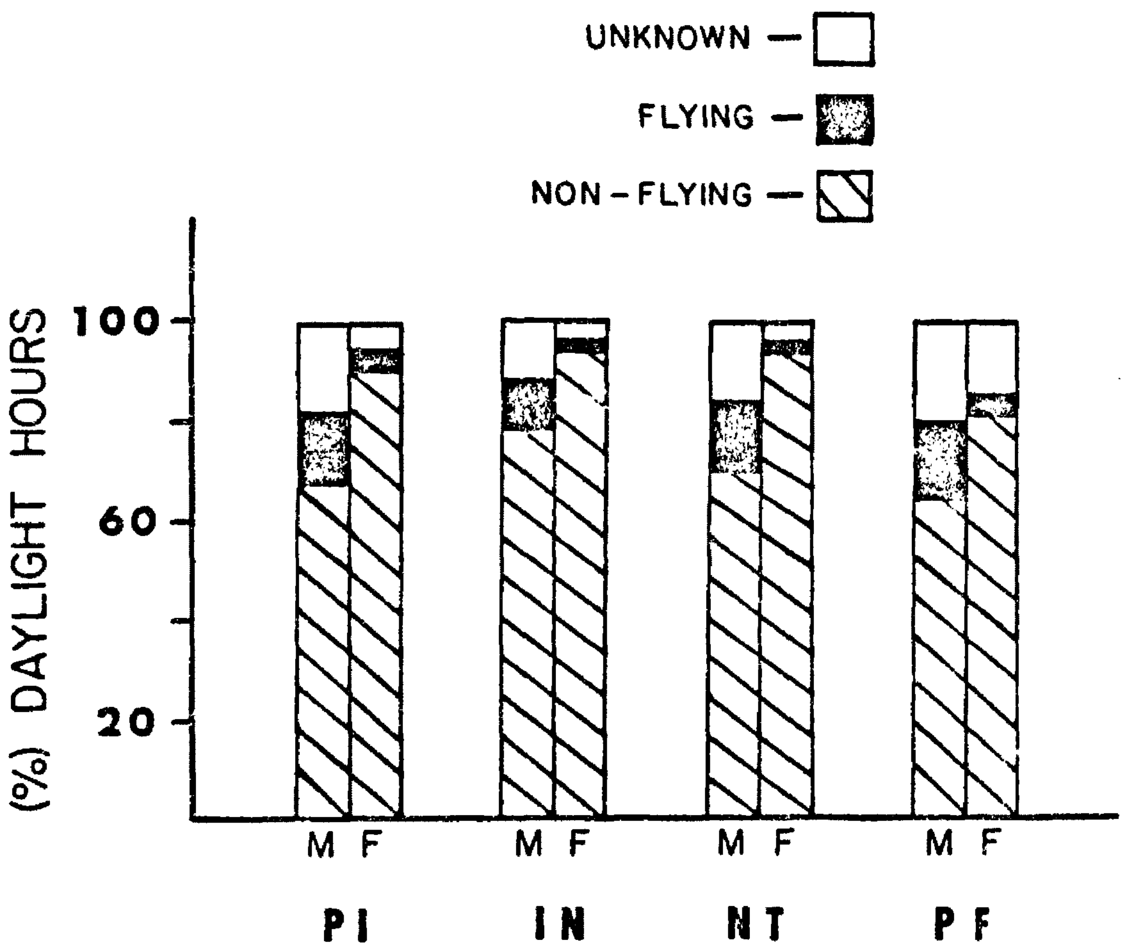

Figure 7. Approximate percent daylight time ospreys engaged in flying, non-flying, and unknown activities during pre-incubation to post-fledging, 1983-1984. PI = Pre-incubation phase, IN = incubation phase, NT = Nestling phase, PF = Post-fledging phase. M = Males, F = Females.

Activity Patterns

Activity patterns of River and pond ospreys were similar, with the greatest differences being in time spent perching and in unknown activities (Table 6, Figs. 8,9). Pond ospreys were seen perching for more (chi-squared = 5.6, $P < .05$) time than those on the River, which were out of sight for relatively more time than those on the ponds. These differences may be a result of River ospreys perching out of sight of the observer, because visibility of ospreys near River nests was often hindered by dense foliage and/or the curvature of the River.

Male ospreys were typically more active than the females because they supplied virtually all of the fish to females and nestlings during the entire study. Females were responsible for 70-75% of the incubation time, with males incubating the remaining 25-30%, primarily while females fed on fish brought to them by the males.

During the nestling stage, females carried out all brooding of the young and rarely were seen off their nests. Brooding continued for 3-4 weeks after hatching and consisted of the females sheltering the newly hatched nestlings during periods of very hot or cold weather. Females fed themselves and their young on the nests during this period with fish delivered by the males, who on occasion, remained on the nests and assisted in the feeding of the young.

As the time of fledging approached, females spent less time on their nests and more time perched in trees nearby. Young were able to feed themselves 6-7 weeks after hatching and their activity and size greatly increased as fledging approached.

Table 6. Approximate percent of daylight time ospreys engaged in activities during incubation to post-fledging on river and pond habitats, 1984.

	River						Pond					
	IN		NT		PF		IN		NT		PF	
Activity	M	F	M	F	M	F	M	F	M	F	M	F
Perching	30	9	30	29	32	28	44	17	65	16	66	24
Feeding	5	6	10	10	11	11	5	4	10	18	9	11
Courtship Flight	<1	0	0	0	0	0	<1	0	0	0	0	0
Aggressive Flight	1	<1	<1	<1	<1	<1	1	<1	<1	<1	<1	<1
Fishing	5	0	6	0	12	0	5	0	10	0	11	0
Obtaining Nest Material	<1	<1	<1	<1	1	1	3	2	<1	<1	3	3
Nest Maintenance	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1
Mounting	0	0	0	0	0	0	0	0	0	0	0	0
Copulating	0	0	0	0	0	0	0	0	0	0	0	0
On Nest	33	72	3	59	5	50	34	74	4	55	6	41
Unknown	25	12	51	2	37	10	7	2	10	10	6	17
Flying	7	1	7	1	14	1	10	3	11	1	15	4
Non-Flying	68	87	42	97	49	89	83	95	79	89	79	77

Hours Observed: River = IN 35, NT 40, PF 20; Pond = IN 45, NT 55, PF 30.

M = Male, F = Female; IN = Incubation, NT = Nestling, PF = Post-Fledgling.

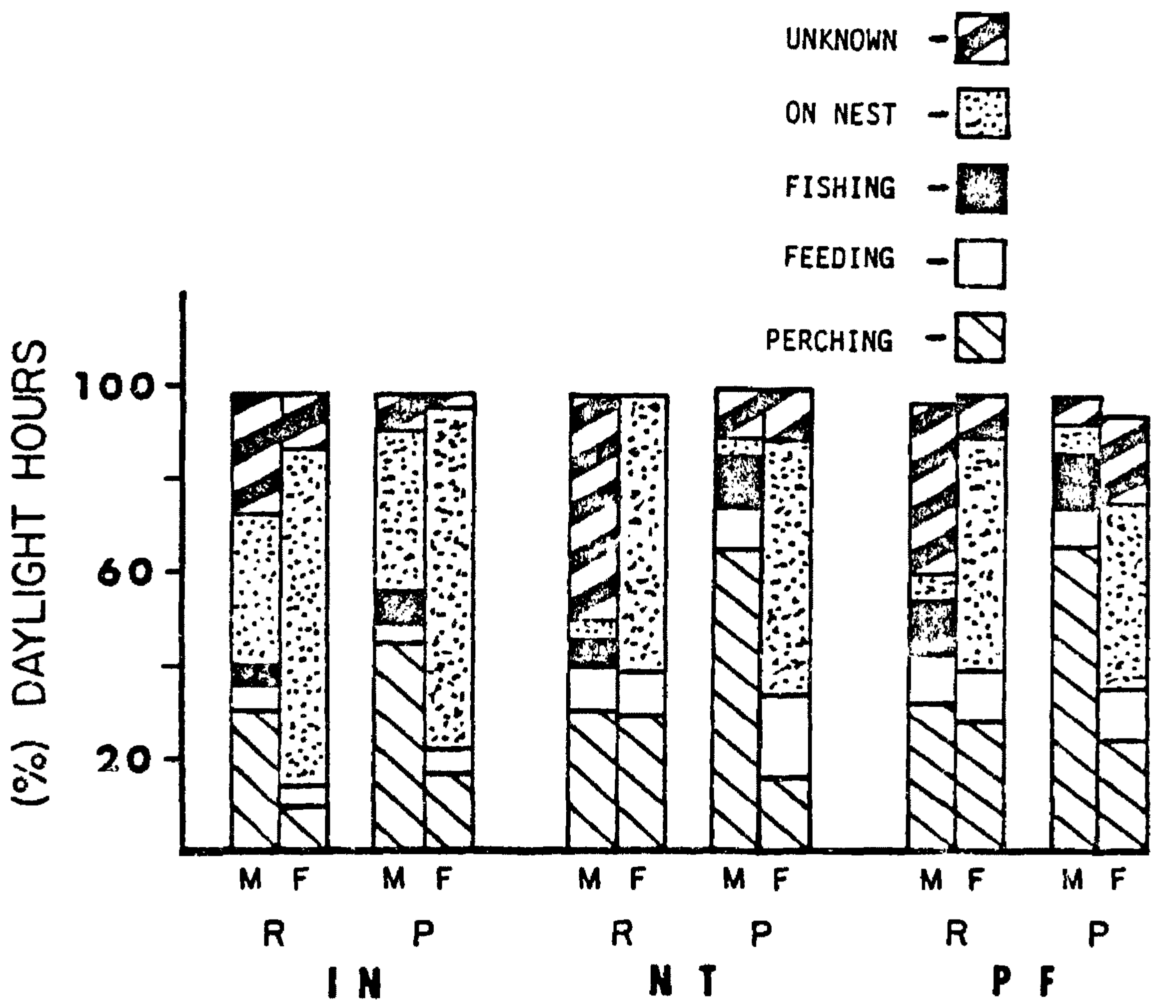

Figure 8. Approximate percent of daylight time ospreys engaged in dominant activities during incubation to post-fledging in river and pond habitats,1984. IN = Incubation phase, NT = Nestling phase, PF = Post-fledging phase, R = River, P = Pond, M = Males, F = Females.

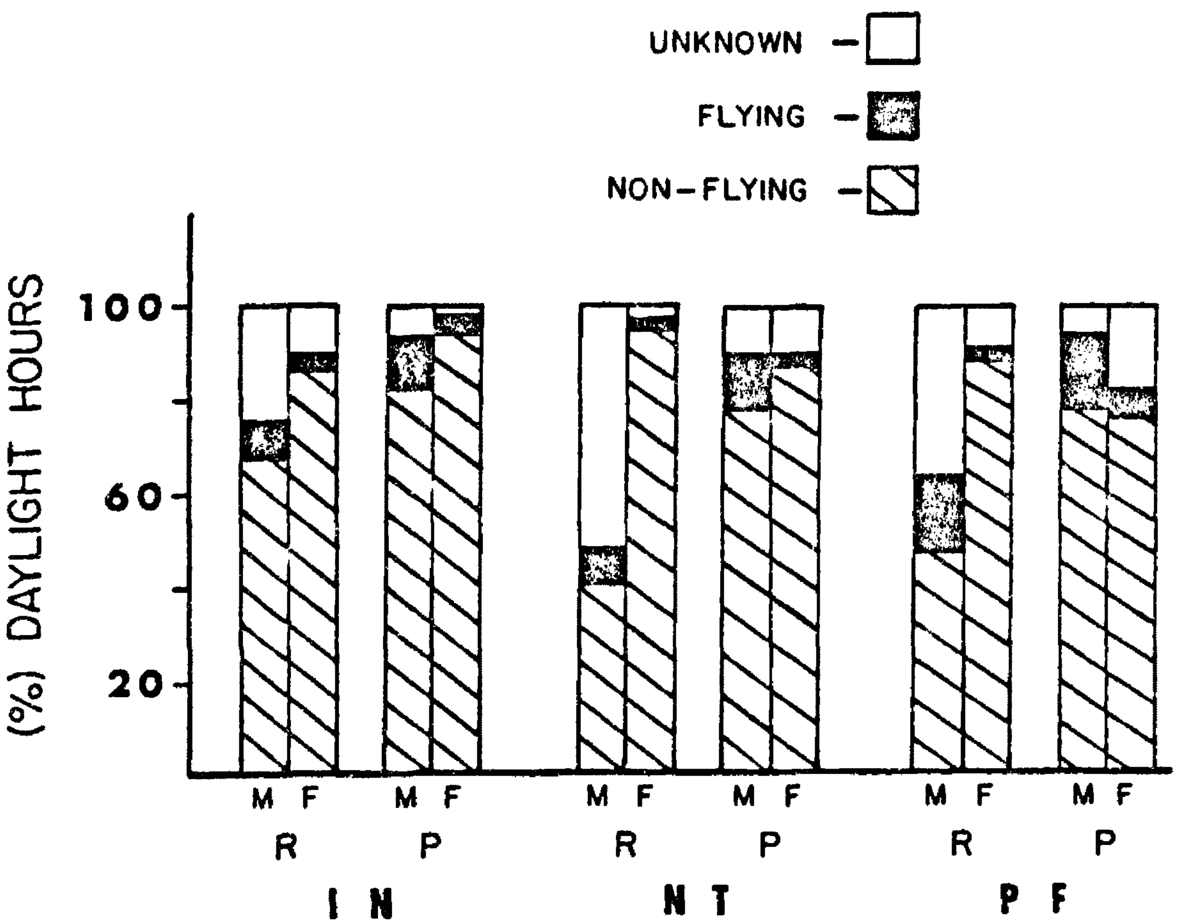

Figure 9. Approximate percent of daylight time ospreys engaged in flying, non-flying, and unknown activities during incubation to post-fledging in river ond pond habitats, 1984. IN = Incubation phase, NT = Nestling phase, PF = Post-fledging phase, R = River, P = Pond, M = Males, F = Females.

During the period just prior to fledging, male ospreys were often seen perched (upwind) near their nests with fish, calling (apparently) to the young on the nests. During these instances the young faced the perching male (into the wind) and began flapping vigorously, calling, often becoming airborne above their nests. These "practice" flights were common at all observed nests, with or without a male present, and began as early as 7 days prior to the first flight from a nest. Most practice flights occurred during periods of high wind and were all carried out facing into the wind. This apparent "luring" by the male ospreys continued for a short period after the fledging of the young, who were then able to land next to or very near the perching male. No instances of food transfer were observed between males and fledglings at perches.

Fledging occurred asynchronously at all observed nests, with 1-3 days between first flights. Such flights often occurred very early in the morning. First flights of fledglings were typically short, and consisted of gliding flights from the nest to a nearby perch below the elevation of the nest. Fledging appeared to be an extension of the practice flights, often being preceded by the flapping, hovering behavior of the nestlings. Landing ability of newly fledged birds was poor, and missed landings were a common occurrence. Only a few days were needed, however, for them to become adept at both landing and taking off. During the first week or so after fledging, the birds spent much of their time flying from perch to perch, ending up on their nests to feed and roost at night. As flying skills increased, they were seen diving and taking extended flights, though no successful fishing attempts were observed. By the 5th or 6th week after fledging, the birds were often out of sight and were very hard to track. Most of the ospreys were gone from their nest areas by the 7th week after fledgling.

Food Delivery

The possibility exists that females from some nests fished, but no such instances were observed. Fishing by the males took from 5-12% of their time from pre-incubation to the post-fledging periods (Table 5, Fig. 8). Percent time spent fishing was essentially the same for river and pond birds, and resulted in similar amounts of food delivered to nests in the 2 habitats (Fig. 10). Numbers and grams of fish/day delivered to each nest increased after hatching and corresponded to the larger number of birds being fed (Fig. 11). Adult-sized birds consumed approximately 250 grams/bird/day during each breeding season. The distribution of fish deliveries, however, differed markedly between habitats (Table 7). Ospreys fishing on the River fished for longer periods of time (chi-squared = 5.2, $P < .05$), fished fewer times/day (chi-squared = 16.7, $P < .001$), and delivered larger fish than did pond ospreys (chi-squared = 9.0, $P < .005$). These results indicate that though fish were more available in ponds, they were smaller in size, thereby requiring more fishing trips/day by the pond ospreys to catch and deliver the weight of fish necessary to sustain their broods. The species breakdown of fish delivered by pond and river ospreys indicates that pond ospreys caught primarily bass and perch while river ospreys

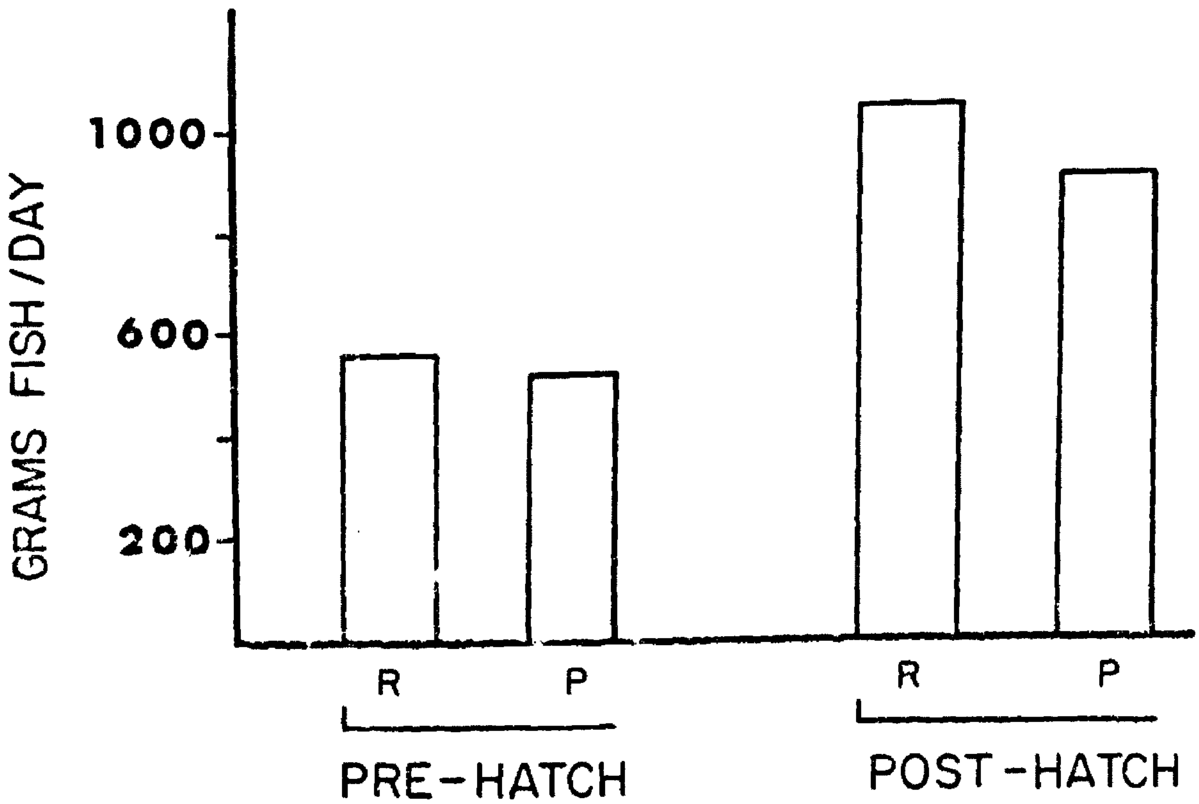

Figure 10. Food delivery rates for river and pond ospreys during early and late breeding season, 1984. R = River, P = Pond.

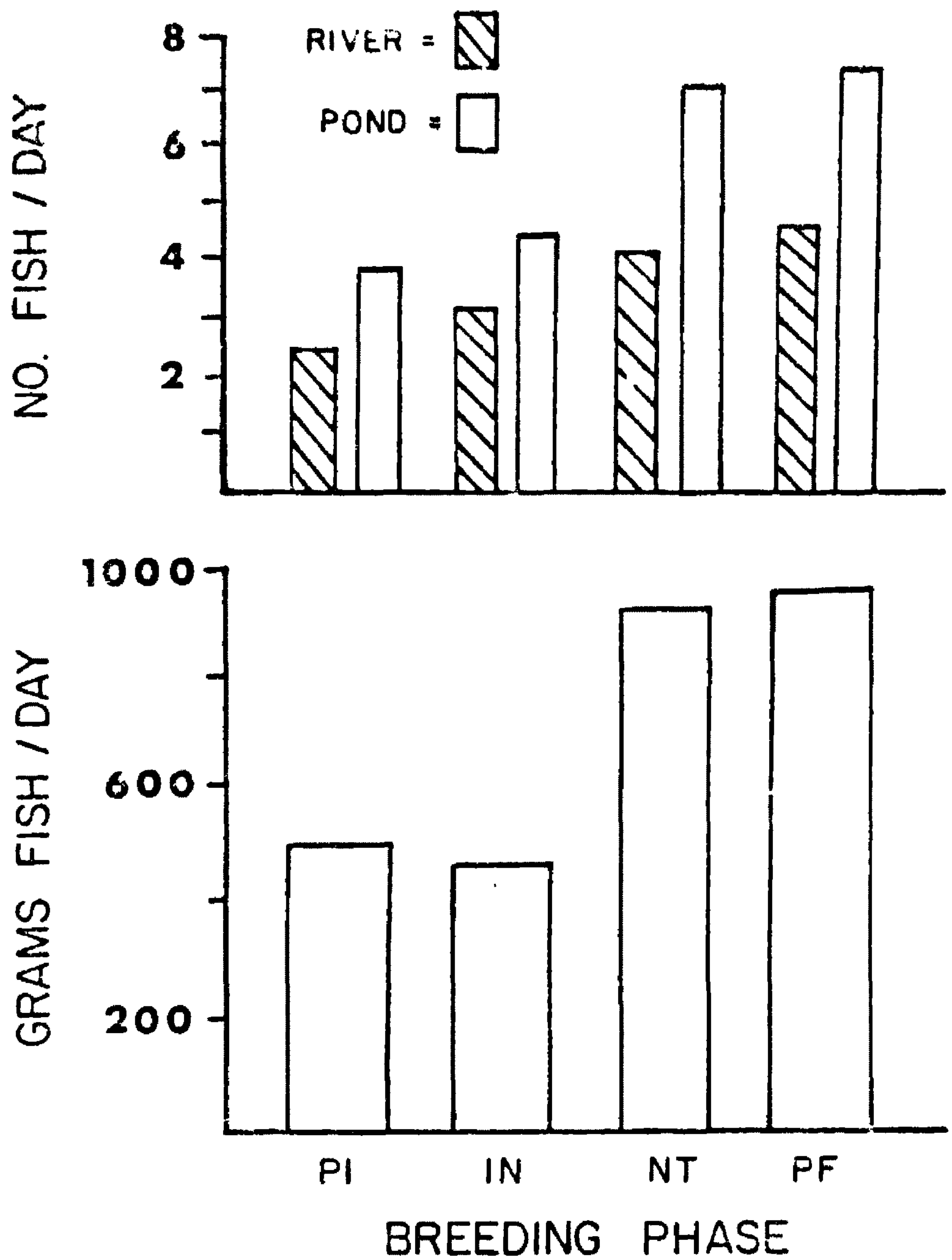

Figure 11. Fish delivery rates by breeding phase for Bitterroot ospreys, 1983-1984. PI = Pre-incubation phase, IN = Incubation phase, NT = Nestling phase, PF = Post-fledgling phase.

Table 7. Distribution of fishing parameters for river and pond ospreys, 1984.

	DT	DST	LC	ETD	LTD
River -	21.5	28.7	25.4 - 30.5	2 -	4
Pond -	8.9	9.9	15.2 - 20.3	4 -	8

DT = Average duration of fishing trips (minutes).
DST = Average duration of successful fishing trips (minutes).
LC = Average length class of fish delivered (cm).
ETD = Approximate number of fishing trips/day in pre-hatch periods
LTD = Approximate number of fishing trips/day in post-hatch periods.

caught trout, whitefish, and suckers or squawfish (chi-squared = 31.9, $P < .001$, d.f. = 3) (Table 8). The similarity and low value of percent time required by pond and river ospreys to catch and deliver fish to their nests indicates that the 2 habitats, while differing in abundance and species composition of fish, supplied adequate and equal amounts of food to these ospreys.

Territorial Defense/Aggression

Time spent defending nests or territories can limit reproduction if defense activities interfere with food gathering or other parental activities. Bitterroot ospreys spent less than 1% of their daylight hours in any form of aggressive activity. Most aggressive encounters, both inter- and intra-specific, took place between male ospreys and "intruding" ospreys, Canada geese, and great blue herons (*Ardea herodias*) from pre-incubation through the time of hatching. Aggressive encounters consisted primarily of defending birds chasing an intruder out of the nest area, while diving and screaming at it. River ospreys were quite active in defending their nest sites against humans on the ground within 50-100 m of their nests.

During the pre-incubation period, female-female encounters took place at 1 river and 2 pond nests. The pond encounters both appeared to be a result of 2 females wanting the same nest. The fights lasted from 2 to 4 hours and consisted of chasing and diving by the 2 females during which time both landed on the nest numerous times.

Table 8. Familial distribution of fish caught by Bitterroot Ospreys, 1984.*

	Salmonidae	Catostomidae	Percidae	Centrarchidae
Pond -	5 (10.6)**	4 (8.5)	22 (46.8)	16 (34.9)
River -	10 (71.4)	4 (28.6)	0	0

* identified by observations in air or at feeding perches.
** Numbers in parentheses indicate percent of total by habitat.

Males took no part in these encounters and usually perched near or even on the nest during them. The situation at the 1 river nest involved 2 pairs of ospreys, one of which occupied the nest in question (pair A), and the other, which was attempting to build a nest on a bridge structure 300 m upstream from it (pair B). Pair B did not successfully complete a nest and was seen in the area of pair A throughout the duration of the 1984 season. Numerous encounters between both birds from both pairs occurred, though pair A was able to successfully fledge 2 (of 3) nestlings. Sporadic acts of aggression occurred throughout each breeding season, and usually involved males chasing other ospreys that had flown too close to a nest or fishing territory.

Defense of fishing territories occurred on the Refuge ponds during both study seasons and appeared to be an extension of nesting territory defense. Most pond ospreys fished in water adjacent to and even underneath their nests, and sometimes dove directly from perches on or near their nest trees. Males from adjacent nests sometimes teamed up to chase intruders from the areas where their fishing territories overlapped. See Figure 12 for approximate distributions of known nesting and fishing territories on the Refuge ponds.

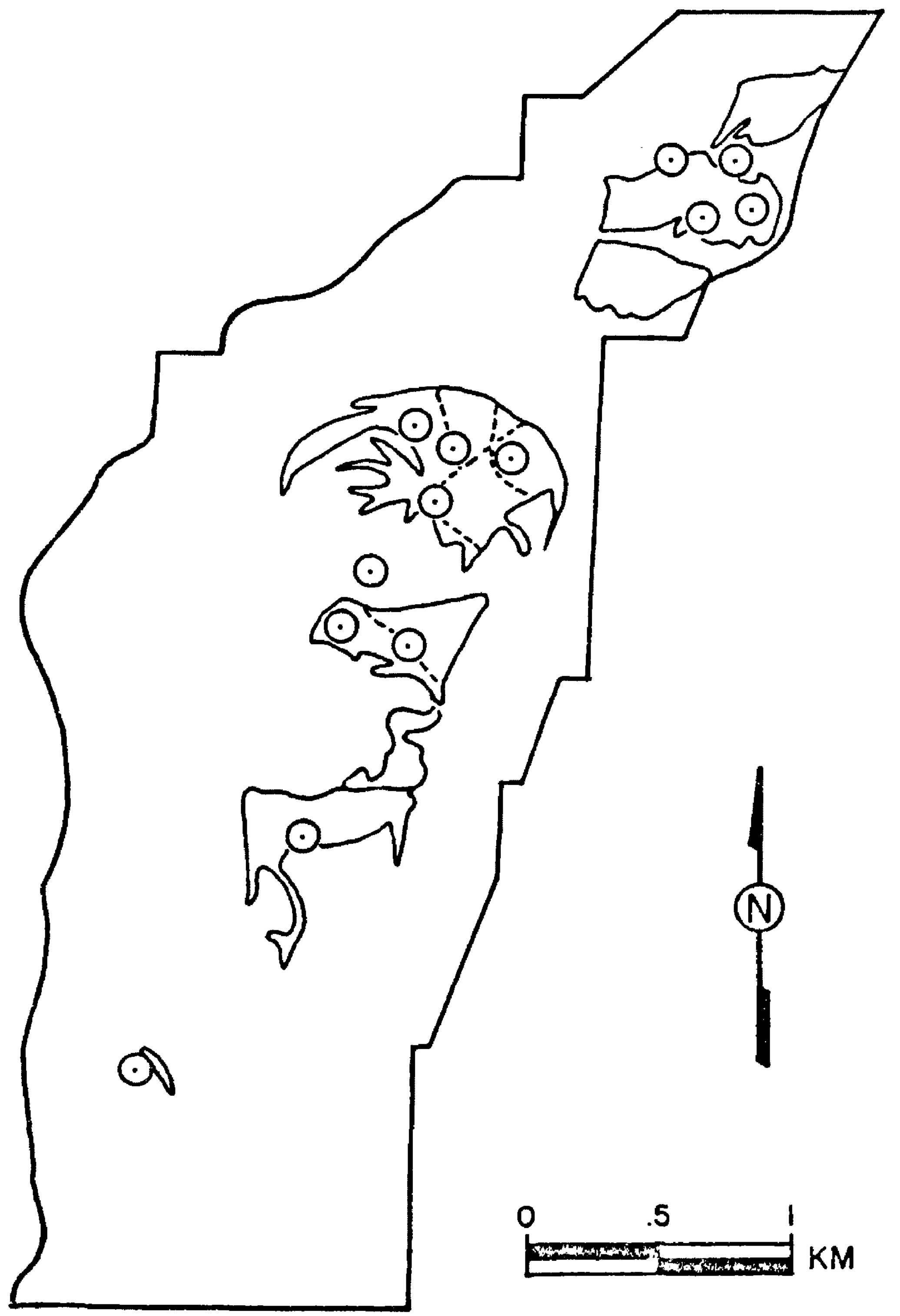

Figure 12. Distribution of osprey nesting and fishing territories on Lee Metcalf National Wildlife Refuge. Known fishing territories are depicted as dotted lines surrounding nest sites.

Nest-Site Characteristics

Table 9 shows nest site characteristics of 10 pond nests measured in 1983 and 15 river nests measured in 1984. Average distance to water was not included in the results because 24 of the 25 nests measured were situated on or within 20 m to water. Nest trees along the River averaged taller than pond nest trees (chi-squared = 12.15, $p < .001$) and had correspondingly greater DBH (chi-squared = 23.88, $p < .001$). Pond nests were relatively more exposed than those on the River (Ranking in stand, Table 9), and were all apex nests, as compared to 87% apex for river nests. Numbers of perches on or near nest trees were similar for the 2 habitats, but species composition and condition of nest trees differed (Table 9, Fig.13). Nine of the 10 pond nests were in ponderosa pine snags, while 13 of 15 river nests were in black cottonwood snags. The difference in species of nest trees was apparently related to the availability of snags rather than to preference by the ospreys. Most snags along the River were black cottonwood while alomst all snags on the Refuge were ponderosa pine. Two osprey nests not included in these data were constructed on power poles during the study, 1 was successful both years and 1 was occupied in 1983.

Table 9. Summary of nest site characteristics for Bitterroot ospreys, 1983-84.

Habitat (N)	Tree ht. (m)	Nest ht. (m)	DBH (cm)	A	R	P	S C P	D
River -	19.96	19.32	83.90	86.7	1.7	1.8	87-13	67.0
Pond -	14.00	14.00	67.10	100.0	1.0	1.8	10-90	100.0
Total -	17.58	17.19	77.18	92.0	1.4	1.8	56-44	80.2

A = % nests in apex of nest tree
R = Average ranking in stand
P = Average number of perches on nest tree
S = Nest tree species percent
D = Percent of nest trees dead

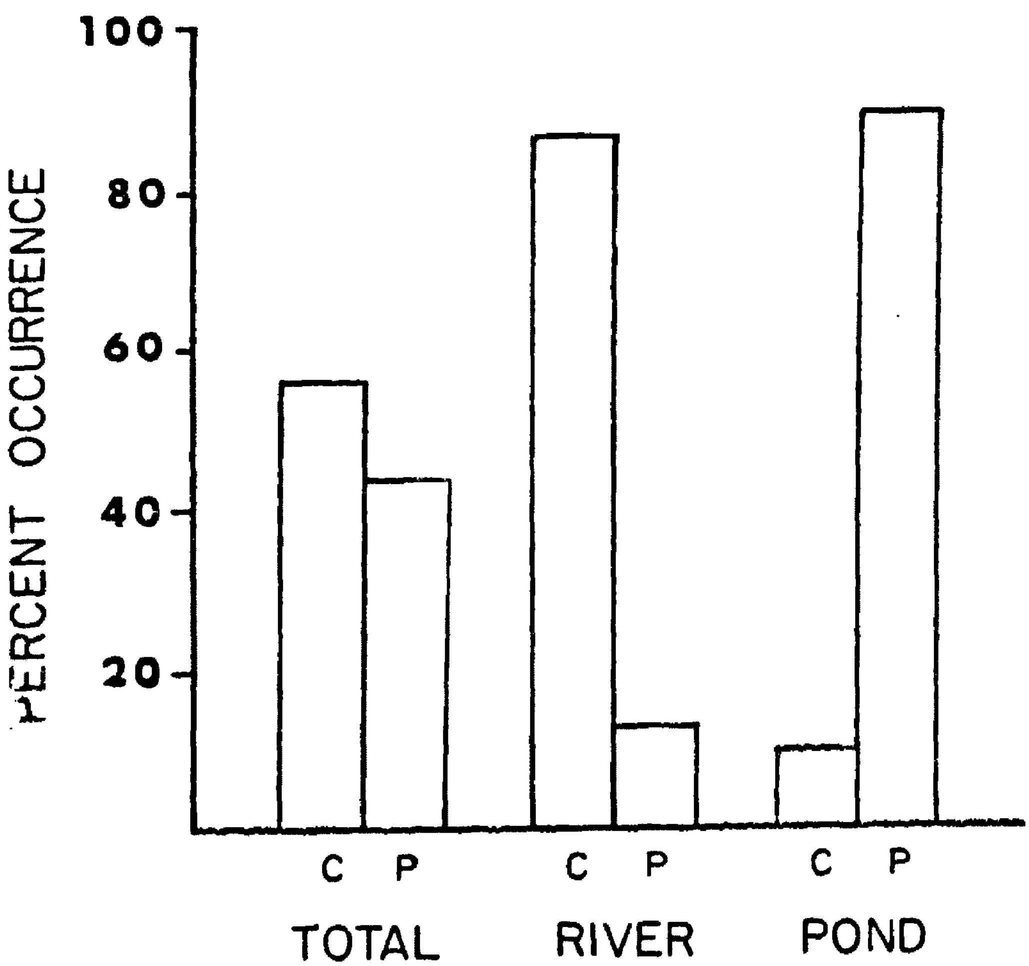

Figure 13. Species distribution of osprey nest trees in the study area. C = Populus trichocarpa, P = Pinus ponderosa.

Polygyny

One nesting territory contained 2 nests and was occupied by 2 females and 1 male during both breeding seasons. The male courted, fed, and copulated with both females at each of their nests. In 1983, 1 female (nest A) laid no eggs, though incubation activities were carried out by both the male and the female on the nest. The other female (nest B) laid 3 eggs and successfully fledged 3 young. In 1984, the female from nest A laid 4 eggs, all of which survived to fledge, while nest B was lost in a windstorm before the eggs (if any) could be counted. The unsuccessful female left the nesting area each year approximately 1 week into the nestling period, and was fed by the male until she left. In 1984, the male copulated with female B the day after her nest was lost, on the site where the nest had been, though no renesting occurred.

Alternate/Frustration Nests

Alternate nests were present in 19 of the 49 (7/22 in 1983, 12/27 in 1984) occupied territories during the study and were used primarily as perching or feeding sites by both males and females where they occurred. Some alternate nests existed from year to year, though in most cases they were a result of "new" nest construction in response to Canada geese nesting in existing osprey nests. In only 1 case was a second nest built after the onset of incubation, that being constructed during the post-fledgling phase in 1983 by an unsuccessful pair.

DISCUSSION

The Breeding Season

The breeding season of ospreys in the Bitterroot Valley is typical of ospreys nesting in similar latitudes worldwide, with the first arrival to the breeding grounds and the beginning of the pre-incubation period in March or April (Bent 1937). Incubation lasts 30-40 days, followed by a nestling period of 50-60 days. After fledging, osprey family units gradually break up preceding fall migration in September.

The length of the pre-incubation period varies for individual nests in a population, and is typically expressed for a population as the average number of days from date of arrival to the laying of the first egg. The pre-incubation period for Bitterroot ospreys was 25 and 20 days for the 1983 and 1984 seasons, respectively. The shorter period in 1984 was due to an earlier date of clutch initiation that year. For ospreys nesting in Scotland from 1959-1973, Green (1976) calculated an average pre-incubation period of 12 days. Levenson (1979) found a difference of 13 days in the average time between arrival and egg laying in 2 osprey populations nesting in northern California. He suggested that climatic variability may be a factor acting to shorten the pre-incubation period of Eagle Lake ospreys in relation to that in climatically moderate Humboldt County.

A variation on this situation occurred in the Bitterroot Valley during my study, where climatic variation may have induced later Canada goose nesting in 1984 than in 1983, although ospreys nested earlier in 1984. Swenson (1979) found that ospreys nested later in Yellowstone National Park during years when weather conditions caused later dates of ice-out, implying a weather dependent date of clutch initiation rather than date of arrival.

The probability that a minimum period of nest occupation prior to egg laying is required to ensure mating success is suggested by Beer (1973) and Follett (1973, in Levenson 1979). They suggest that an increasing number of mating attempts prior to egg laying (see Fig. 6) may aid in the synchronization of the hormonal systems of the 2 sexes.

In a monogamous species such as the osprey, in which pair bonding is presumably long-lived, this pre-incubation period may become shorter as the number of seasons a pair are together increases. Ospreys apparrently return to the same nest site year after year, and members of a pair usually return within a few days of each other (Allen 1892, Ames 1964, Green 1976). Thus, the courtship period of 20-25 days exhibited in the Bitterroot Valley may reflect the minimum time necessary, under the worst of conditions (inclement weather in migration, mate loss, etc.) and may be unduly long under "normal" conditions. A pre-incubation period of whatever length is thus necessary to ensure that both sexes are on the breeding grounds prior to egg laying, to synchronize mating readiness in both sexes, and to maintain and defend established nesting sites from previous years.

Many factors probably act to regulate timimg of the osprey breeding season in the different geographic regions of the world. Among these factors are dates of ice-out, timing of prey migrations, and high water peaks that affect food availability. As gene pools adapted to these local conditions, they have probably become dependent on them. This idea should therefore be taken into consideration when changes in the "system" (dams, canals, etc.) are being considered.

Reproductive Success

Spitzer (1980) calculated a reproductive success rate of 0.79 fledglings per active nest/year as that needed to maintain osprey population stability. Previous to Spitzer's work, Henny and Wight (1969) calculated a replacement rate of 0.95-1.3 fledglings per active nest/year. The reproductive rate for a recovering osprey population between New York City and Boston from 1969 to 1979 was 0.53-1.35 fledglings per active nest/year (Spitzer and Poole 1980). This suggested that population growth began at a reproduction rate similar to that calculated by Spitzer (1980).

The reproductive rate for Bitterroot ospreys of 1.89 fledged per active nest per year is well above the suggested replacement level, and probably indicates a growing population. A 3-fold increase in the number of nests in the valley during the past 10 years (Robert Twist, Dennis Flath, pers. commun.) supports this conclusion.

Osprey populations throughout the northern Rocky Mountains are all exhibiting similar patterns of growth. Reported reproductive rates are all comparable to that in the Bitterroot Valley: 2.0-2.4/successful nest in the Flathead Valley (Klaver et al. 1982); .44-1.31/active nest in the Yellowstone-Teton National Park Complex (Swenson 1979, Alt 1980); 1.2-1.7/active nest on the upper Missouri River (Grover 1984); and 1.0-1.6/active nest in Long Valley, Idaho (Van Daele and Van Daele 1982). Numbers of breeding ospreys have essentially doubled during the past 10 years along the rivers and lakes of northwestern Montana (Dennis Flath, Ray Washtak, pers. commun.).

Reasons for these recent increases in numbers of nesting ospreys may be many. Certainly, the formation of reservoirs, as discussed by Swenson (1981a), Flook and Forbes (1983), Grover (1984), and others, has played a key role in providing attractive osprey habitat. Reservoirs may be partially responsible for the increases, but the river systems in the region are experiencing similar trends. This leads to speculation that some other factor(s) may also be involved in these dramatic increases.

The coincidence of increases in population sizes and reproductive rates since the early 1970s with the discontinued use of DDT is a factor that cannot be ignored. Available data on historic osprey populations for much of the region are virtually non-existent, making any predictions on population declines speculative at best. Data from Lake Coeur d'Alene, Idaho (Johnson et al. 1975), Flathead Lake, Montana (MacArter and MacArter 1979), and Yellowstone National Park (Swenson 1979) do, however, indicate trends of decline and recovery coincidental with the use and discontinued use of DDT, suggesting that similar trends may have occurred elsewhere in the region.

Food Availability

The influence of food availability on osprey reproductive success has been discussed in the literature (Koplin et al. 1972, Poole 1981, Flook and Forbes 1983, Grover 1984). Poole (1981) showed conclusively that reduced food delivery rates can have a negative impact on osprey nestling survival, and if pronounced, can cause starvation among nestlings. Poole recorded instances of sibling aggression among nestlings, resulting in the preferential feeding of older, larger young. This brood reduction behavior, one of the first cases documented for ospreys, only occurred in populations limited by food. Koplin et al. (1972) found data suggesting lower osprey productivity in oligotrophic than in mesotrophic lakes. Their conclusions were based on the fact that fish were less available in oligotrophic lakes. No sibling aggression or instances of preferential feeding were seen in the Bitterroot population, suggesting that food was not limiting these ospreys. (For further discussion see Time-Activity Budget below).

The subject of food availability also arises in the discussion of "enhanced" osprey population sizes around reservoirs (Grover 1984) and man-made marsh impoundments (Flook and Forbes 1983, pers. obs.). Grover (1984) found significantly higher nesting osprey densities on reservoir portions than on river segments of the upper Missouri River. Differences in prey species taken by ospreys in the 2 habitats

(Catostomidae on rivers, Percidae on reservoirs), were also found. Grover (1984) suggested that these results indicated a difference in prey species composition, availability, or both, possibly making reservoir habitat "more desirable by allowing the birds to more easily meet their energy demands." Flook and Forbes (1983) found, on the Creston Valley Wildlife Management Area (CVWMA), that marsh impoundment enhanced fish productivity, and may have been responsible for a 2-fold increase in the osprey breeding population since 1968.

The situation in the Bitterroot Valley is quite similar to that on the CVWMA, where the formation of the Refuge impoundments has resulted in a 3-fold increase in the Bitterroot osprey population. In addition to a large supply of fish, the Refuge impoundments have resulted in the formation of hundreds of snags (see study area description), some of which have since become osprey nest trees. Species composition of fish taken by pond and River ospreys in the Bitterroot are quite similar to Grover's (1984) data above (see Results-Food Delivery Rates for comparison). The relative ease with which pond ospreys caught fish was only balanced by the larger fish caught by those nesting on the River. If River ospreys had more trouble catching fish, I could agree with Grover's conclusion.

An interesting and potentially important phenomenon was noted by Spitzer and Poole (1980), whereby established colonies of ospreys gained more than twice as many new nests as did those in isolated locations. Potential reasons for this fact are discussed by the authors, and include the food availability at colony sites and the "semi-social" nature of ospreys. The authors did not, however, indicate relative densities of ospreys in the 2 areas, a factor that could explain the results on the basis of recruitment alone. The importance of this phenomenon, if is exists, is that newly established reservoir "colonies" could attract more and more ospreys to themselves as time goes on, resulting in even larger population increases than would be expected otherwise.

Human Disturbance

The debate as to whether ospreys are or are not disturbed by human activity has a long and arduous history, and may never end. Instances of ospreys nesting on chimneys, barns, power poles, almost any structure, and in many situations, are recorded throughout the literature. These ospreys have undeniably adapted to co-exist with man, but one must be wary of assuming the same adaptability for the species in general.

Many studies of osprey populations in the western United States (Swenson 1979, Van Daele and Van Daele 1982, Levenson and Koplin 1984) have shown that decreases in osprey productivity can be directly related to high levels of human activity. The extent of these effects apparently depend on the timing of the disturbance during the breeding season, and changes in the level of disturbance as the breeding season progresses. Opsreys initiating nesting near human "activity" may be more tolerant of it than those initiating nesting in relative seclusion. A pattern of this type was evident for the Bitterroot population. Ospreys nesting near roads or houses were tolerant of noise and activity near their nest sites, while those nesting in relative seclusion were overtly aggressive toward humans as far as 150 m from their nests. Depending on the duration of an interaction, reproducive success of ospreys showing this aggressive response could be affected if incubation or brooding activities were seriously interrupted. An example of the adaptability of ospreys to man-caused disturbance was manifest by ospreys on the Refuge ponds, in particular, those nesting near the approach corridor of the Refuge Manager's airplane. When attempting to count eggs and/or nestlings during the 2 seasons, a very effective method of flushing ospreys from their nests was to fly once over the nest and quickly circle back while the bird was off the nest. Aparrently, because they were used to low-flying aircraft, the birds nesting near the approach corridor were hard to flush and only left their nests after repeated attempts to flush them were made.

Inclement Weather

The effects of weather on osprey reproduction can vary from changing the date of nest initiation, and possibly reproductve success (Swenson 1979, Van Daele and Van Daele 1982)(see above), to totally destroying nests containing eggs and/or nestlings (MacCarter and MacCarter 1979, Ray Washtak, pers. commun., pers. obs.). The overheating/cooling of eggs and nestlings can occur, and probably depends on clutch and brood sizes, and/or the level of disturbance at a nest site. The effects of a severe windstorm can be quite drastic in that the possibility of many nests being wiped out in 1 storm always exists. Susceptibility to wind certainly seems to vary among osprey nests, and in the Bitterroot depends on both the exposure of the nest and the condition of the nest tree. The propensity of ospreys to nest in exposed areas around lakes, rivers, or shorelines, coupled with their preference, in general, for dead trees as nest sites, makes the species quite susceptible to reproductive failure at the hands of the elements.

Time-Activity Budgets

Time-activity budgets make possible the analysis of energy allocation, division of labor, and parental investment of breeding animals (Levenson 1979). Time-budget analyses for ospreys are available since the mid-1970s for several populations, including Scotland (Green 1976), Virginia (Stinson 1978), northern California (Levenson 1979), and Nova Scotia (Jameison et al. 1982). Time-budget analyses were carried out for the Bitterroot population to determine what factors might influence the breeding success of the population. One of the potential limiting factors for any species is that of food availability. The time spent foraging by ospreys should indicate the relative availability of food to a population.

Food Delivery

Poole (1981) found that reduced food delivery rates had a negative influence on nestling survival, and concluded that food abundance was the primary cause of the reduced food delivery rates. Poole discussed the relationship between time spent by males fishing and the availability of food, which may be inversly proportional under most levels of food availability. However, due to a possible "energetic ceiling," osprey foraging time may become maximized at the food availability level corresponding to this "ceiling." The fact that male ospreys spend from 70-90% of their time in non-flying activities (Levenson 1979, this study), has led others to speculate that the energy or the "dive-stress" involved in the fishing behavior of ospreys somehow limits their number of fishing attempts/day (Stinson 1982). The evolutionary importance of these limitations is that given the long life span of ospreys, a particular male may be able to produce more young over a period of years, if yearly survival is enhanced by "resting" much of the time (Poole 1981).

Males in the Bitterroot spent from 5-12% of their time actively fishing, which I earlier concluded was an indication of readily available food. The fact that some Bitterroot ospreys fished from perches, as described for Minnesota ospreys by Dunstan (1974), introduces another aspect to the discussion of foraging energetics of these birds. In habitats where ospreys can perch near fishing sites and actually "fish" at the same time, energy spent foraging can be greatly reduced with no negative influence on fishing success. Populations not afforded this luxury may then experience food stress, on the basis of energy expenditure alone, at availability levels similar to those of birds able to take advantage of perches over fishing sites. Males fishing from perches probably require less food/day than those actively fishing, and are then able to supply more of each fish to the females and nestlings.

Van Daele and Van Daele (1982) present calculations that adult and fledgling ospreys require approximately 268 and 254 grams of food/day respectively. From these data, a nest with 2 adults and 3 young would require approximately 1300 grams of fish/day. Most data in the literature indicate daily food delivery rates similar to this hypothetical figure (Green 1976, Stinson 1978, Levenson 1979, and others), although reproductive success figures for these populations show 2 young and 2 adults as typical. Poole (1981) found that nests in food-stressed populations received 800-900 grams/day while 1400 grams/day were delivered to nests in healthy populations. Food delivery rates for the Bitterroot population (Figs. 9, 10) correspond to the calculated required amounts for nests with 2 young and 2 adults (approx. 1000 gr/day), which corresponds to the average brood size for this population. The higher values of food deliveries in the studies above may reflect the duration of observation periods from which the calculations were made. I contend that data from observation periods less than 8 continuous hours tend to overestimate numbers and therefore grams of fish/day delivered to nests for a population. Because ospreys do not fish uniformly throughout the day (Green 1976, Stinson 1978, this study), numbers of fish/hour multiplied by hours/day might not be an accurate measure of number of fish/day if data from only a few hours of continual observation are involved.

Aggression/Defense/Predation

Another important result obtained from time-budget analyses is the time spent by animals defending nest sites from potential predators. The very small amount of time spent by Bitterroot ospreys in any type of aggressive encounter indicates that aggression played a very small role in the reproductive behavior or success of the population.

The possibility exists that avian predators such as common ravens (Corvus corax), great blue herons, great horned owls (Bubo virginianus) are able to exploit osprey eggs (MacCarter and MacCarter 1979). The absence of predation may be the reason for the historically large numbers of ground-nesting ospreys on Gardiner's (Bent 1937) and Plum islands (Allen 1892) on the east coast of the U.S. A large number of great horned owls, herons, and red-tailed hawks (Buteo jamaicensis) inhabit the Bitterroot Valley, and were sometimes seen perched or flying near osprey nests during the study. Three instances of egg and/or nestling loss (not obviously weather induced) occurred during this study, though the causes of the losses are unknown.

Nest-site Characteristics

Because of the adaptability of ospreys to the use of artificial nest sites and the changes in available habitat brought about by man, documenting the characteristics of osprey nest sites in pristine environments is of interest (Swenson 1981b). The current expansion of osprey populations taking place in the West makes the question of suitable nesting habitat an important one. Nesting habitat may be the ultimate determinator of the extent to which these expansions will continue to occur. As is evident for the Bitterroot population, the creation and retention of snags after reservoir formation can cause large increases in osprey numbers in a relatively short period of time. Areas of this type, with readily available food and snags, may form base populations from which further expansion and colonization can proceed. The retention of "characteristic" habitat along the river systems may be important to ensure the the osprey's future in the West.

CONCLUSIONS

Ospreys in the Bitterroot Valley are currently reproducing at rates well above that required for replacement. This is supported by the fact that the population size has been steadily increasing since the early 1970s. The discontinued use of DDT and the formation of reservoirs have apparently been responsible for osprey increases, not only in the Valley, but throughout much of the United States. The roles of habitat, food availability, and human disturbance as regulators of reproduction are becoming more important to researchers as the population dynamics of ospreys are better understood, and will play an ever increasing role in the management of western ospreys.

Recent changes in public attitudes toward non-game species have been responsible for an increased emphasis on not only the research and management of non-game species, but the value of their "place" in the ecosystem. An example of this change in public attitude, not previously discussed in this thesis, is the fact that the shooting of ospreys was not uncommon prior to the advent of "modern" thinking. The extent to which shooting affected population levels is certainly not known, though the declines discussed previously may have been enhanced by it.

The future of ospreys in the West looks very positive at this point, and depends to a large extent on the continuation and enhancement of public education, state and federal non-game programs, and an inherent awareness of the value of the wildlife around us.

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