

Osprey distribution along the Upper Missouri River : ideal free
by Peter John Harmata

A thesis submitted in partial fulfillment of the requirements for the degree Master of Science in Fish and Wildlife Management
Montana State University
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Abstract:
The Ideal Free Distribution (IFD) predicts that when animals colonize a habitat, individuals will settle in the higher quality patches first. As density increases on these higher quality habitats, competition lowers average intake rates and fitness making it beneficial for arriving individuals to colonize lower quality patches. Individuals which inhabit these lower quality patches, attain equal average intake rates and fitness as those individuals on the higher quality habitat, due to decreased competition. The IFD model assumes that: 1) animals have an "ideal" perception of the habitats and patches available to them; 2) individuals are "free" to enter and inhabit any habit or patch without significant time or energy exertion; and 3) the patches of habitat the population of a species inhabits differs in some measurable way in terms of quality. In 1984 and 1992, two ecological surveys of osprey were conducted along the Upper Missouri River, Montana from Townsend, MT downstream to Wolf Creek, MT. The 1992 study, discovered similar relative densities of nesting osprey as that found in 1984 but with significant increases on two sections of the study area. These two sections were believed to be of lower quality. I measured the density of nests on sections/patches of my study area, delivery rates of fish to nestling osprey (estimate of intake), reproductive success, size and species of fish delivered to nests by male osprey, and I analyzed fish data from each section to determine if sections differed in prey availability. Delivery rates differed among sections (4 sections) of the study area. Mean reproductive success (fitness) of birds on each section was equal across sections. Fish data indicated that osprey were taking suckers (Castostomus spp.) more than was expected based on proportion of fish delivered. Fish data also indicated that the relative number of fish caught on 3 sections of the study area did not change since 1984. In conclusion, from the data I gathered osprey seem to conform to the predictions of the EFD, with the patch/section designation I applied.

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of

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This thesis has been read by each of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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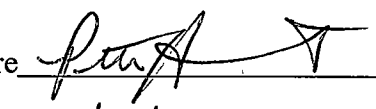
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ABSTRACT

The Ideal Free Distribution (IFD) predicts that when animals colonize a habitat, individuals will settle in the higher quality patches first. As density increases on these higher quality habitats, competition lowers average intake rates and fitness making it beneficial for arriving individuals to colonize lower quality patches. Individuals which inhabit these lower quality patches, attain equal average intake rates and fitness as those individuals on the higher quality habitat, due to decreased competition. The IFD model assumes that: 1) animals have an "ideal" perception of the habitats and patches available to them; 2) individuals are "free" to enter and inhabit any habit or patch without significant time or energy exertion; and 3) the patches of habitat the population of a species inhabits differs in some measurable way in terms of quality. In 1984 and 1992, two ecological surveys of osprey were conducted along the Upper Missouri River, Montana from Townsend, MT downstream to Wolf Creek, MT. The 1992 study, discovered similar relative densities of nesting osprey as that found in 1984 but with significant increases on two sections of the study area. These two sections were believed to be of lower quality. I measured the density of nests on sections/patches of my study area, delivery rates of fish to nestling osprey (estimate of intake), reproductive success, size and species of fish delivered to nests by male osprey, and I analyzed fish data from each section to determine if sections differed in prey availability. Delivery rates differed among sections (4 sections) of the study area. Mean reproductive success (fitness) of birds on each section was equal across sections. Fish data indicated that osprey were taking suckers (*Castostomus spp.*) more than was expected based on proportion of fish delivered. Fish data also indicated that the relative number of fish caught on 3 sections of the study area did not change since 1984. In conclusion, from the data I gathered osprey seem to conform to the predictions of the IFD, with the patch/section designation I applied.

INTRODUCTION

The ability to predict how animals will distribute themselves across habitats has important implications for population ecology, evolution, and wildlife conservation (Brown 1969; Orians 1969; Fretwell and Lucas 1970; Fretwell 1972; Parker 1970, 1974). The most influential body of theory concerning animal distributions across landscapes of patches of different suitabilities is the Ideal Free Distribution (IFD) [Fretwell and Lucas 1970]. The IFD predicts that the best or most suitable patches, in terms of food intake and reproduction, are selected and occupied first (Fig. 1). As density increases on the most profitable patches, competition causes intake rates and/or reproductive success to decline and less profitable patches become occupied. These less profitable patches become occupied to the point where the average intake rate on all patches equalizes.

The IFD predicts that individuals will attain equal intake rates over patches of differing suitability and/or profitability. But, as Petit and Petit (1996) describe, determining or demonstrating *a priori* measurable differences between habitats can be inherently difficult. Traditional methods of determining differences in suitabilities of habitats (i.e., density or other apparent measures of preference) do not take into account true differences in habitat quality such as nest site availability, vegetative structure, food abundance, or predation risk. Reproductive success has also been used *a posteriori* to support the initial estimates of habitat suitability, but if true habitat differences have not been determined independent of fitness, then determining if a species adheres to the predictions of the IFD cannot be done.

In the simplest IFD model, patches consist of continuously arriving resources that

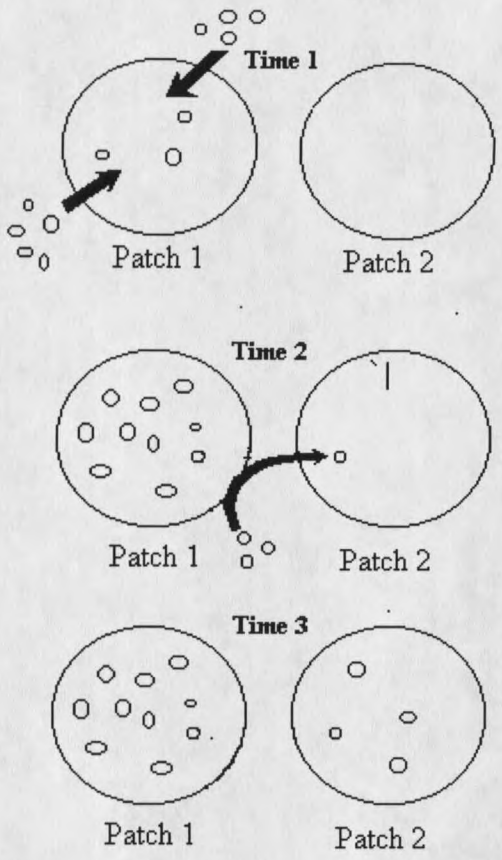


Figure 1. The manner in which the IFD predicts animals will colonize patches of habitat with different inherent qualities, in terms of prey availability, nest site availability, and survival rate. Time 1, individuals colonize Patch 1, the patch that will maximize their fitness (Patch 1> Patch 2 in terms of quality/suitability/profitability). Time 2, as density increases on the best patch (i.e., Patch 1), individual intake rates decline through competition (interference or exploitation) and less suitable patches increase in their suitability. Time 3, individuals colonize the less suitable patch (Patch 2). Lower density on Patch 2, allows incoming individuals to attain an equal intake rate to Patch 1.

are "consumed" immediately (i.e., continuous input patches) (Tregenza 1994). The prediction from this simple IFD model is that the proportion of individuals in a patch equals the proportion of resources entering that patch, but for these predictions to hold,

animals must meet certain assumptions. The IFD assumes that animals distribute themselves "ideally" in patches (i.e., have a perfect knowledge of the resources/benefits within patches) and are able to travel freely to, or settle in any patch, uninhibited by competitive interference (e.g., territoriality) [Fretwell and Lucas 1970]. Few studies have tested IFD predictions in natural settings and the results have been equivocal (Parker and Sutherland 1986; Tregenza 1995). Tregenza (1994 & 1995) states that the key shortcoming of most IFD studies is the attempt to apply continuous input predictions to animals whose resource base is non-continuous. In natural settings an individual's prey is usually dispersed and an individual must search to find it (Tregenza 1994). Thus, subtle changes in the number and rate by which prey enter a patch may not result in a proportional increase in predators and contradict the predictions of the continuous input IFD.

Additionally, many studies have confused the input matching rule (Parker 1978), which predicts that the number of competitors in a patch should be proportional to the total input received by that patch, to the prediction that animals should have equal intake rates across patches (Tregenza 1994). The problem with applying the input matching rule is that it only applies to continuous input systems and animals in natural settings could very well be achieving numbers proportional to the input to the system, but not attaining equal intake rates and thus not achieving an Ideal Free Distribution. Tregenza (1994) describes that the confusion between the input rule and intake rates has resulted in many researchers concluding that certain species conform to the predictions of the IFD while not actually measuring and recording individual intake rates on different patches.

Applying the principles of the IFD to raptors is of theoretical and practical interest

because food and nest site availability limit distributions of raptors (Newton 1979). Specifically, breeding ospreys (*Pandion haliaetus*) are good subjects for tests concerning the IFD because of the ease of locating large conspicuous nests and of recording productivity and feeding rates. Osprey also do not defend foraging territories (Greene 1987; Poole 1989; Flemming et al. 1991) thus, they are "free" to enter a patch on an equal basis as residents (i.e., without restriction or costs in terms of time and energy wasted from interference interactions) (Tregenza 1995). Consequently, density of other individuals, not behavior, precludes individual birds from attaining maximum energy intake. Lastly, osprey are a large raptor capable of long sustained flights (Poole 1989) allowing them to attain, as close as possible, "ideal" knowledge of the patches available to them with minimal time and energy costs.

Preliminary investigation of osprey distribution on the Upper Missouri River presented an opportunity to determine if osprey adhere to the predictions of the IFD. In the early 1980's, Grover (1984) determined the distribution and reproductive status of ospreys along four sections of the Upper Missouri River: Holter, Hauser, and Canyon Ferry Reservoirs and one free flowing river section (River). Nest density was highest on Canyon Ferry Reservoir followed by Hauser, Holter and the River. Grover (1984) hypothesized that this nesting distribution reflected prey availability. In 1992, Restani and Harmata (1992) surveyed the same study area and found that osprey nested in the same relative densities as in 1981-1982 (Grover 1984). However, the most significant increase of occupied nests was recorded on the River and Hauser Reservoir sections. These sections were previously hypothesized to contain less prey. The number of nests

on Canyon Ferry and Holter Reservoirs remained relatively constant.

In my study, to determine if osprey on the Upper Missouri River met the requirements of the IFD, I focused on four characteristics: prey abundance, nest sites, foraging success and delivery rate, and productivity. Prey abundance was used to test if patches (sections) of my study area differed in a manner suggested by Grover (1984) and Restani and Harmata (1992). Nest sites and the change in their distribution over time would indicate if the population had increased and whether a higher density of individuals occurred on the hypothesized higher quality patch. Foraging success and delivery rates would then indicate if birds on my study area were achieving equal feeding rates across these patches of differing quality. Delivery rates as an indication of intake rates also alleviates the concerns and problems expressed by Tregenza (1994) of determining whether a species conforms to the predictions of the IFD. Lastly, the production of young across my study area sections/patches would indicate if these birds were achieving equal reproductive outputs while residing on patches of differing quality. If all these were met, then I could conclude that the osprey on my study area were distributed in an Ideal Free manner.

A fundamental question arises from Grover's (1984) and Restani and Harmata's (1992) investigations: Does osprey nest site selection on the Upper Missouri follow IFD predictions? To answer this question five requirements must be met: 1) Quality of patches must differ. 2) A higher density of individuals must reside in the best quality patch. 3) The population's nesting distribution changes across patches, in response to an increased density of individuals. 4) Fitness must be equal across patches, and 5) Intake

rates must be equal among sections.

STUDY AREA AND METHODS

The study area comprised a 196 km section of the Upper Missouri River from Three Forks, Montana downstream to Wolf Creek, Lewis and Clark County, Montana (Figures 2-4). The study area contained four dams: Toston Dam, Canyon Ferry Dam, Hauser Dam and Holter Dam. Toston Dam, located 37 km upstream from Canyon Ferry Reservoir, is a low head diversion dam whose purpose is to provide water for irrigation and to provide electrical power. Toston Dam has little storage capacity and fluctuates greatly in its discharge (MFWP 1992). Canyon Ferry Dam, a storage dam, has a storage capacity of 2.509 Billion cubic meters at full pool and provides electrical power, flood control, municipal water, irrigation, and recreation for the surrounding area (MFWP 1992). Canyon Ferry Reservoir experiences severe water level fluctuations throughout the year and releases from Canyon Ferry Dam determine flow patterns in downstream reaches (MFWP 1985). Hauser and Holter Dams are run-of-the-river hydropower dams.

Fish populations on the study area are dominated by white sucker (*Catostomus commersoni*) and longnose sucker (*C. catostomus*), carp (*Cyprinus carpio*), rainbow trout (*Salmo gairdneri*), brown trout (*S. trutta*), mountain whitefish (*Prosopium williamsoni*), and yellow perch (*Perca flavescens*) [Holton 1990].

Land use varies from agricultural and recreational to mining and logging. Recreational activity (fishing and boating) on the three reservoirs is extremely high,

especially on Canyon Ferry and Holter Reservoirs (MFWP 1985). Canyon Ferry reservoir is the most heavily used body of water in the state for recreational activity (MFWP 1992). The River portion is rarely used for recreation (Ron Spoon pers. comm.). The climate of the study area is semiarid.

Nesting Distribution and Productivity

I conducted the study from May to August 1998 and 1999. I conducted four aerial surveys (May and July each year) to determine early and late season nest site occupancy and activity. An occupied nest/nesting territory was any nest where at least one of the following occurred: young were raised, eggs were laid, one adult was observed sitting low in the nest, presumably incubating, or two adults were present on or near the nest (Steenhof 1987). I used Global Positioning System (GPS) to plot osprey nest sites on 1:100,000 Bureau of Land Management maps. The number of young produced each year was determined from flights, boat, and vehicle. Each nest was visited on the ground to reduce the error caused by relying solely on fixed-wing aircraft for determining productivity (Ewins and Miller 1995).

To index nest site availability, I obtained power line maps of the study area from Montana Power Company (MPC) and the Vigilante Co-op unit. These data were obtained because osprey have developed a high affinity for nesting on power poles (see Van Daele and Van Daele 1982; Austin-Smithand and Rhodenizer 1983; Poole 1989). A differential increase by study area section in power lines and power poles since 1983

might explain a shift in osprey distribution. Maps included lines installed back to the 1950's, but exact installation dates could not be determined for most lines.

Lastly, I measured nestlings to determine if a difference in habitat quality might be expressed across sections of river through body condition. I recorded head length (nearest 0.1 cm), wing chord (nearest 0.1 cm) and mass (nearest gram). An index of body condition was estimated by dividing mass by head length and wing chord. These measurements have been used traditionally to determine body condition of eagles (Bortolotti 1984; McClelland et al. 1998).

Prey Abundance

I used MFWP spring (May) floating gill netting data (1986-1999) to rank habitat quality of the three reservoirs. I assumed that spring floating gill netting data was representative of available prey because the breeding season of osprey on the Upper Missouri River extends from April to the first week in September.

MFWP spring floating gill-netting data were also analyzed to determine if fish abundance had changed since Grover's (1984) study. Annual sampling of the reservoirs did not start until 1986, thus data only existed from 1986 to 1999. I assumed that data from 1986 represented fish numbers during Grover's 1981-82 field seasons because no major changes in angler pressure had occurred (Dave Yerk, MFWP, personal communication).

Due to the differences in fish sampling methods used between the River and the

reservoirs, I used MFWP electroshocking data to estimate the quality of the River. Electroshocking techniques sample fish within the upper depths of water and were consequently considered available to the birds on the River section (Reynolds 1996). The reservoir with the highest number of fish caught was considered the highest quality habitat (Cuthbert and Rothstein 1988). Lastly, I assisted MFWP in electroshock sampling during the spring and fall of 1998 and 1999 to determine relative fish abundance and species composition of the River section (Reynolds 1996).

Foraging Behavior and Prey Selection

I determined prey delivery rates of adult male osprey to nests to determine if the quality of foraging habitat differed among sections and was expressed in a manner other than prey availability. I conducted nest watches by study area section. Each section was given a number (1-4) and the initial section monitored was chosen randomly each year and successive sections were sequential. Thus, if Holter Reservoir (Section 4) was randomly selected first, the River (Section 1), Canyon Ferry reservoir (Section 2), and Hauser reservoir (section 3) would follow for that year. I observed nests in 4 hour time periods from 0500-2100 hours to obtain a representative sample across daylight hours. A "run" constituted observing all four sections for each time period. A section was completed only after all time periods had been observed.

I used a 40X scope to observe prey deliveries to nests from a vehicle or boat within 90 meters of nests. I estimated the length (cm) of fish in reference to the adult

male osprey's body (Machmer and Ydenberg 1990; Carss and Godfrey 1996). I also recorded the species of fish and time of delivery. I had difficulty distinguishing between species of suckers (white and longnose) and between species of trout (brown and rainbow), so I combined these into a "Sucker" category and a "Trout" category. The remaining species of fish [i.e., yellow perch, mountain whitefish, walleye (*Stizostedion vitreum*), Utah chub (*Gila atraria*), and carp] were grouped into an "Other" category. These five species were common to Canyon Ferry and Holter reservoirs, but on Hauser reservoir the "Other" category also contained kokanee salmon (*Oncorhynchus nerka*).

I estimated the weight of fish delivered to nests using regression analyses between lengths and weights of known fish (Anderson and Neumann 1996). Known rainbow and brown trout lengths and weights were used from electrofishing conducted on the River section during the spring of 1998 and 1999. All other lengths and weights used to estimate the remaining species' weights, were obtained from MFWP gill netting data from 1998 and 1999 per reservoir. Estimates of the slope and intercept that resulted from these regression equations were incorporated into the equation $\log_{10}(\text{weight}) = a' + b$ $[\log_{10}(\text{length})]$ specific for each species (Anderson and Neumann 1996). The antilogs of the results of these equations were then taken to give actual mass in grams.

I collected prey remains under nests at the conclusion of each nest observation period (Van Daele and Van Daele 1982; Grover 1984). Prey remains were also collected at the end of the season opportunistically from other nests. I constructed a reference collection of these diagnostic bones (i.e., opercle, cleithra, and pharyngeal teeth) for

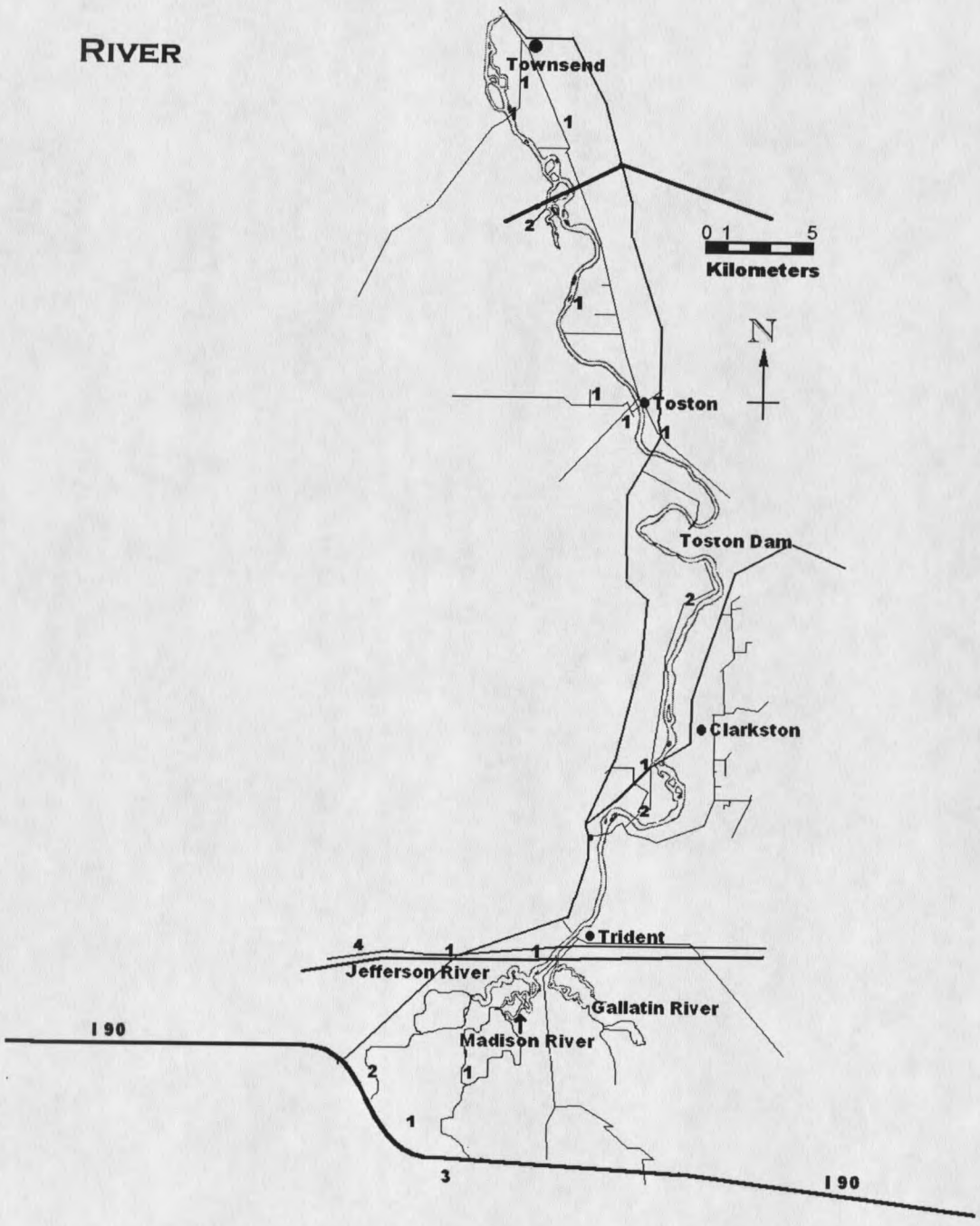


Figure 2. The River section of the Missouri River and associated osprey nest sites and distribution. Numbers represent different years of occupancy: 1= Occupied during 1998 and 1999, 2= Occupied only during 1998, 3=Occupied during 1999 only, and 4= New nest discovered in 1999.

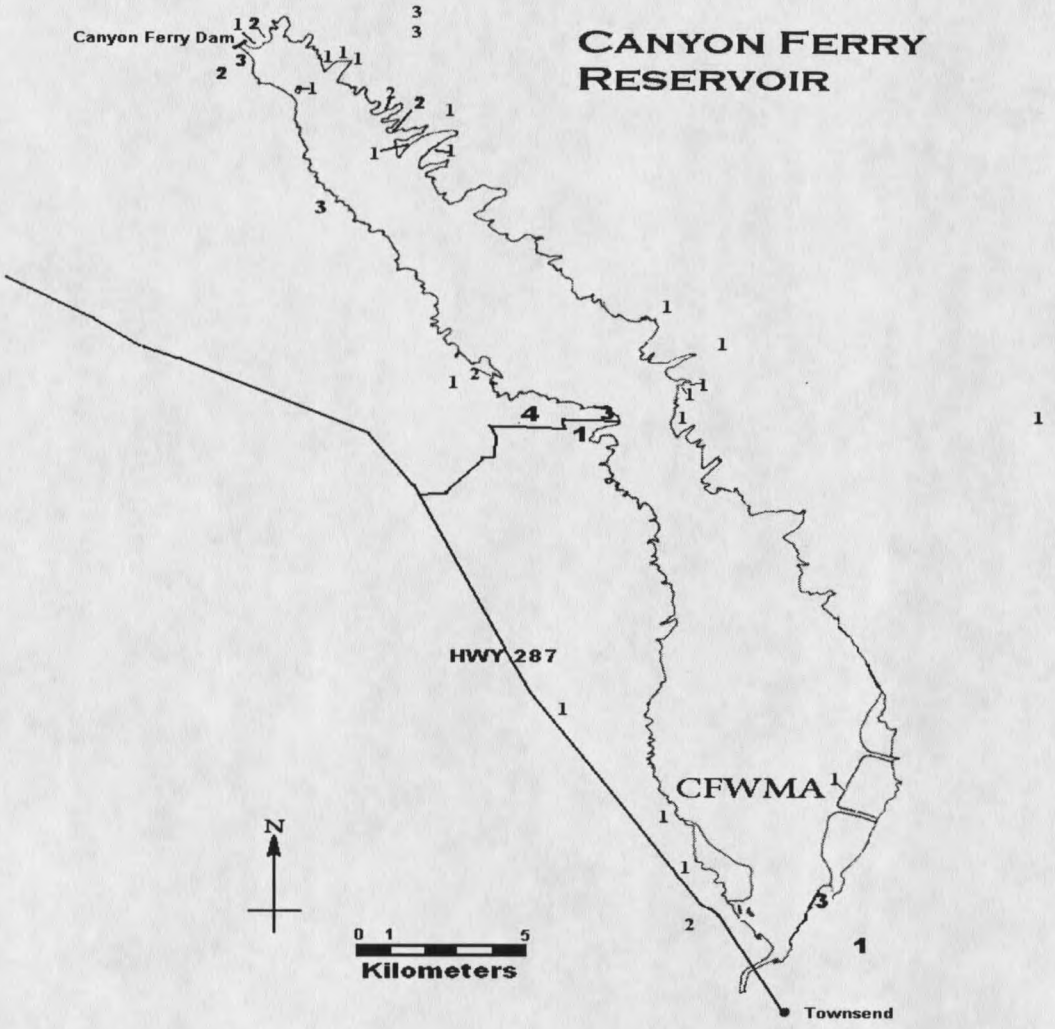


Figure 3. Canyon Ferry Reservoir with associated occupied osprey nest sites and distribution. Numbers represent differing years of occupancy: 1= Occupied during 1998 and 1999, 2= Occupied only during 1998, 3=Occupied during 1999 only, and 4= New nest discovered in 1999.

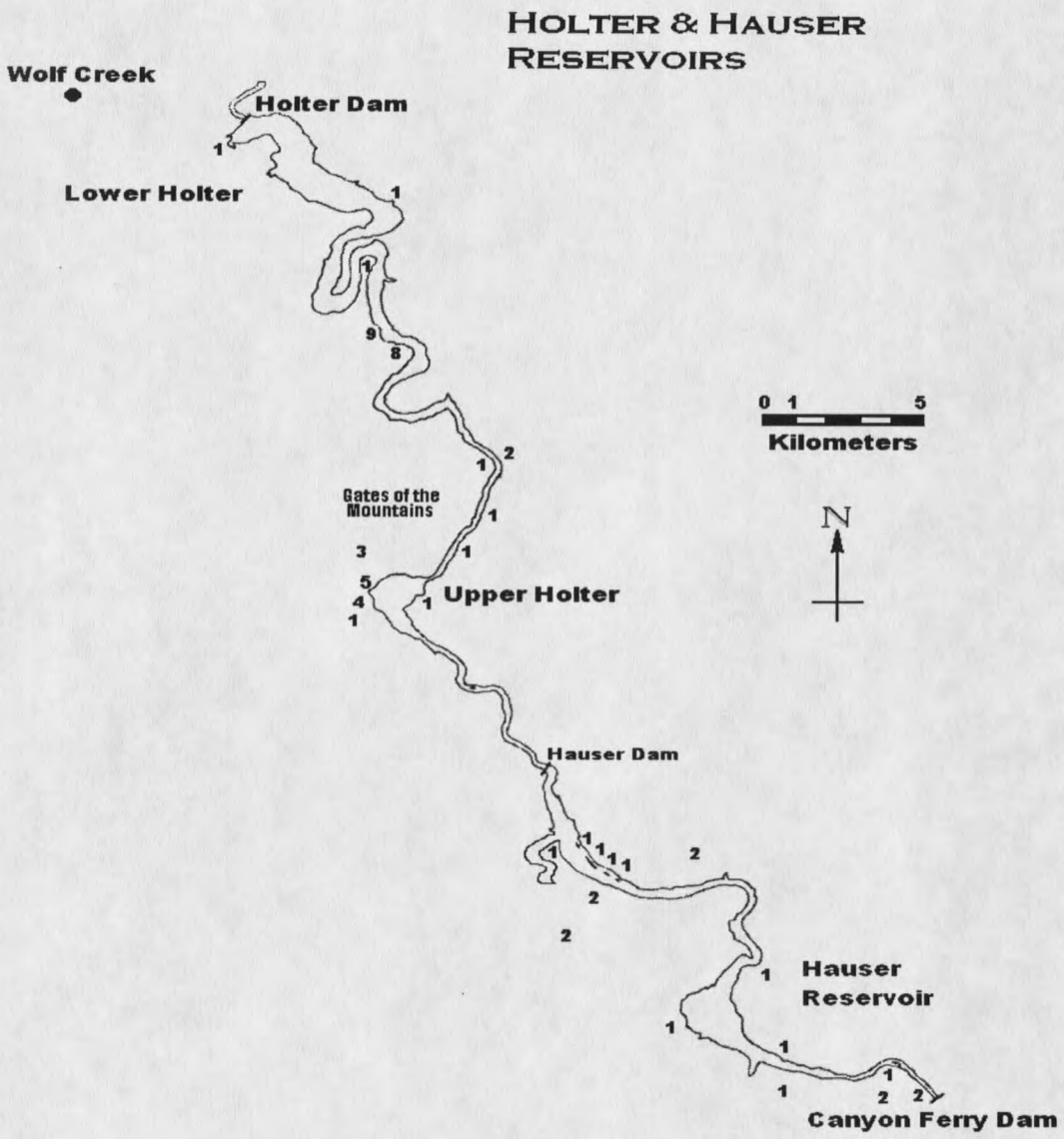


Figure 4. Holter and Hauser Reservoirs and associated occupied osprey nest sites and their distribution. Numbers represent differing years of occupancy: 1= Occupied during 1998 and 1999, 2= Occupied only during 1998, 3=Occupied during 1999 only, and 4= New nest in 1999.

identification of primary prey species (Frost unpublished report 1996; Gould 1997; Zollweg 1997).

In 1999, I quantified the foraging success of osprey on the study area in relation to foraging effort using two measures. First, adult male osprey from each study area section were observed for the same time periods as delivery rates. The nests of observed male osprey, were chosen randomly as described above. An assistant and I followed birds in a boat and used stopwatches to estimate the amount of time (seconds) an individual male spent flapping and soaring. The number of successful and unsuccessful dives was also recorded. Males were followed until they returned to the nest or until they were lost from view. Secondly, I also recorded the amount of time adult males spent away from the nest as another index of foraging effort. Because of poor weather, low water levels on the River section, and the difficulty in following adult males for an extended period of time, I only recorded flapping and soaring data from July to the end of the study during 1999 (2nd week in August).

Statistical Analyses

I used parametric tests unless data failed to satisfy assumptions of normality (Shapiro-Wilk's W Test). Changes in the mean number and distribution of occupied nests over time (1983-1998) were investigated using chi-square tests. Productivity (mean number of young) was compared across sections using one-way Kruskal Wallis-ANOVA (KW-ANOVA) tests. I pooled data across years due to small sample sizes within years.

I tested for differences in mean prey delivery rates of adult male osprey across

sections using KW-ANOVA tests. Post hoc tests of pair-wise comparisons of non-parametric statistical tests of means were adjusted to account for experiment-wise error using Bonferroni criteria (P-values $< 0.1/6 = 0.017$ were considered significant). Post-hoc non-parametric comparisons of two means were conducted using Mann Whitney U tests.

I compared the mean estimated length of fish delivered by osprey across sections using KW-ANOVA tests. The number of each species of fish delivered to nest sites by male osprey were incorporated into chi-square tests of homogeneity as the observed frequencies to determine if osprey were using/selecting a species of fish more than would be suggested by the availability of that species (Alldredge and Ratti 1986). I pooled data across years because of small sample sizes within years. Preferred and/or selected species of fish by osprey were determined through these chi-square homogeneity tests for the reservoirs and the River section. In contrast to the reservoirs, electrofishing data were used as the number of fish available on the River section.

An important prediction of the IFD states that within a patch the proportion of resources should equal the proportion of foragers. I performed Z-tests of two proportions to test if the proportion of occupied nests on a section of the study area equaled the proportion fish caught on that section via spring floating gill nets.

To determine if the condition of nestling osprey was different across sections of river which might coincide with differences in prey availability, multiple regression analysis was utilized. Sections of the study area were coded (e.g. River =100, Canyon Ferry = 010, Hauser Reservoir = 001, and Holter Reservoir =000) and used as predictor variables. The response variable was body condition (mass/wing chord) of nestling

osprey.

RESULTS

Nesting Distribution and Productivity

The number of occupied nests on each section of the study area increased from 1981-82 to 1998-99, with the greatest increases occurring on the River and Hauser Reservoir (Table 1 and Figure 5). The 1998-99 mean density of nests per kilometer of shoreline on Canyon Ferry was greater than any other section (Table 1). The distribution of occupied osprey nests across sections of my study area changed significantly from 1982 (Grover 1984) to 1998 (χ^2= 47.19, df=3, p< 0.001). Numbers of occupied nests were below expected on Canyon Ferry (z = -2.60, p = 0.005), but higher on the River section (z=2.94, p= 0.003). The proportion of occupied nests each section nearly doubled except on Hauser (Figure 6). The proportion of occupied nests on Hauser did not change from 1982 to 1998 (z = -0.82, p= 0.207).

The number of young produced on each section of the study area increased since Grover (1984) (Table 1). No difference was found between years (1998 and 1999) for any section of the study area regarding the number of fledgling osprey produced (KW-ANOVA p-values all > 0.33). Additionally, no difference was found across sections of study area in the mean number of young produced [KW-ANOVA, H (3, N=152)= 1.75, p=0.63]. Condition of nestling osprey did not differ by study area section either by average mass/head length {KW-ANOVA H [3, N=37(River n = 7, CF = 17, HA = 11, HO

Table 1. Increase in nesting osprey population and productivity on four sections of the Missouri River from 1981-82 (Grover 1984) and this study.

Section	Length (km)[1]	Mean No. Occ.[2] '81-82	Mean No. Occ.[2] '98-99	Mean Density (#Occ/km)[3] '81-82	Mean Density (#Occ/km)[3] '98-99	% Increase In Density	Mean #Yng/OccN[4] '81-82	Mean #Yng/OccN[4] 98-99
River	74	2.0	18.5	0.03	0.25	733.0	0.00	1.11
Canyon Ferry	48	26.0	31.0	0.54	0.64	18.5	1.15	1.23
Hauser	26	3.0	15.5	0.16	0.60	275.0	1.00	1.29
Holter	43	10.5	13.0	0.24	0.30	25.0	1.29	1.35

[1] Kilometer of shoreline in each section.
[2] Mean Numer of Occupied Nests
[3] The number of occupied nests per kilometer
[4] The mean number of young per occupied nest

= 2] = 4.83, p=0.18} or average mass/wing chord (ANOVA- F=0.72, p=0.55).

Foraging Behavior and Prey Selection and Abundance

No difference existed in mean delivery rate across years on each section of the study area (ANOVA-all p-values >0.21; Table 2), so I pooled delivery rate data across years. Canyon Ferry osprey had lower delivery rates (0.2 fish/hr) than River osprey (0.4 fish/hr) [Mann Whitney U p=0.004]. Delivery rates for Holter (0.3 fish/hr) and Hauser (0.3 fish/hr) Reservoirs were not significantly different from either Canyon Ferry Reservoir or the River (Mann Whitney U, all p-values > 0.04) (Figure 7). Contrary to the delivery data, the time spent away from the nest by male osprey did not differ among sections [KW-ANOVA H (3, N=70)=1.07, p= 0.78]. Additionally, the amount of time male birds spent flapping and soaring did not differ among sections [KW-ANOVA H (3, N=19)=1.095, p=0.7783; KW-ANOVA H (3, N=70)=5.06, p=0.17 respectively].

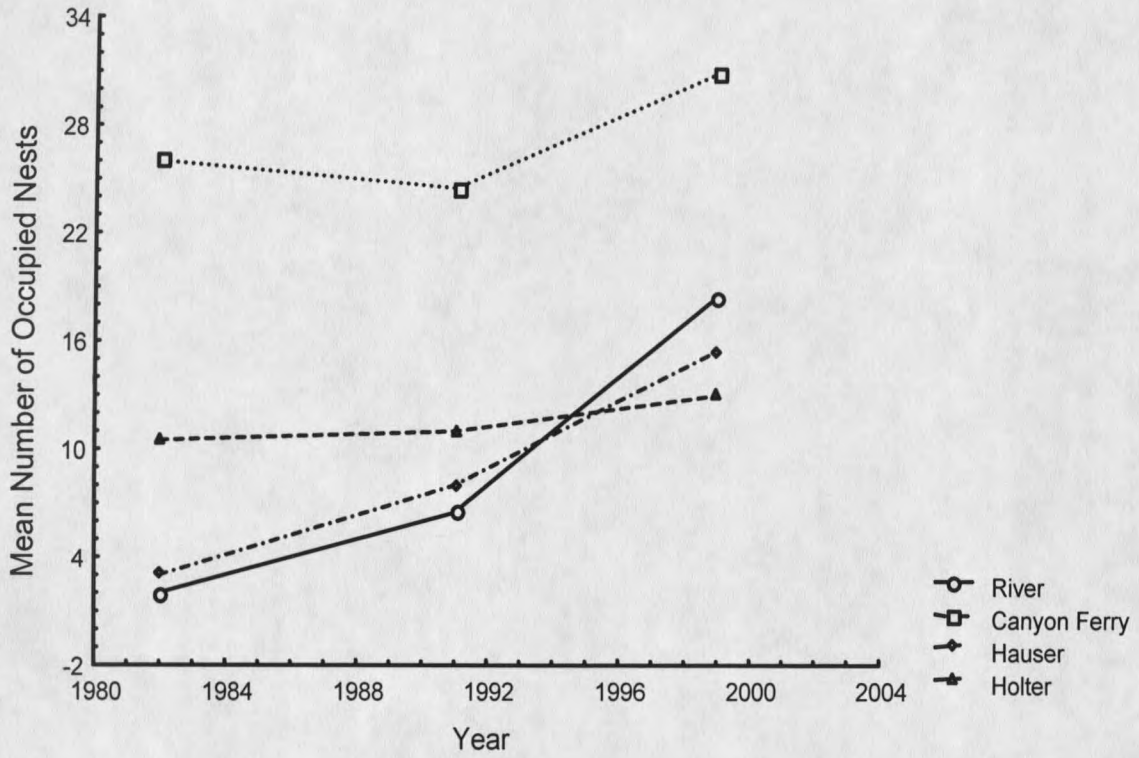


Figure 5. Increase in the mean number of occupied nests over the course of three intensive studies. 1981-82 Standard errors (R=1.41, CF=5.66, HA=1.00, HO= 0.25), 1998-99 standard errors (R=0.25, CF= 0.00, HA=1.00, HO= 0.00). Standard errors were not available for 1991.

River birds also delivered smaller fish than birds foraging on Hauser reservoir but the difference was not statistically significant (LSD test, $p > 0.05$) (Figure 7). No significant difference was found between Canyon Ferry, Hauser and Holter reservoirs in the mean length of fish brought to nests (LSD test, all p-values > 0.13). A significant difference existed across sections in the average mass (grams/delivery)

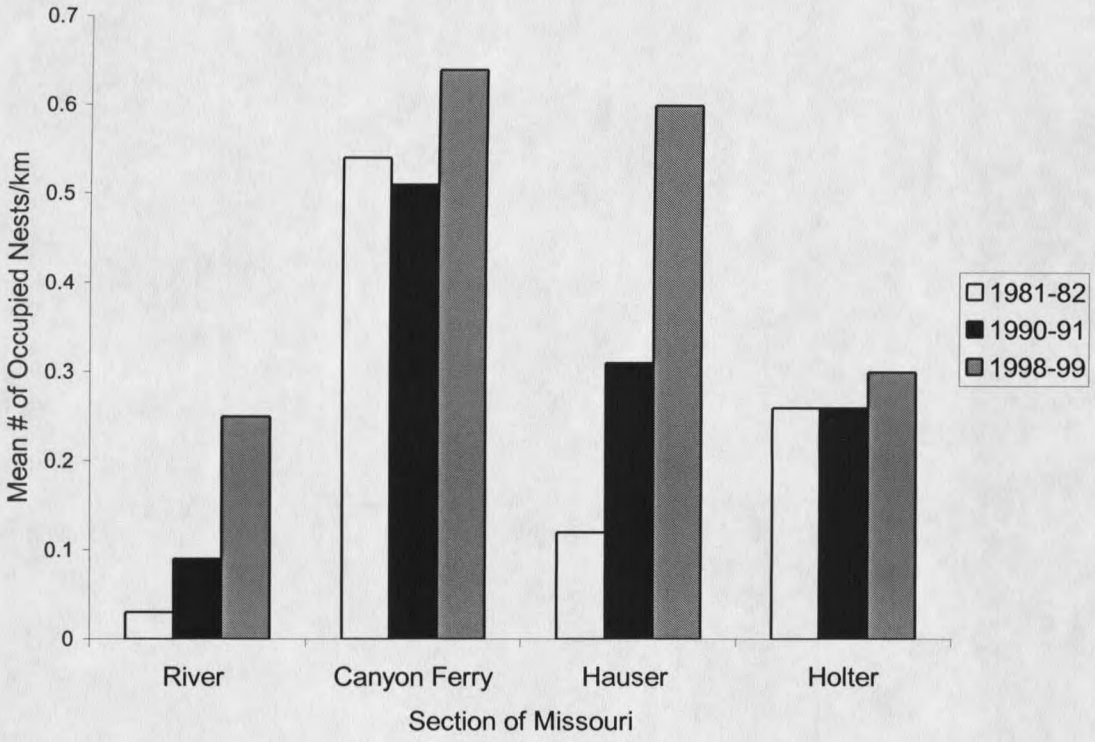


Figure 6. The proportion of occupied nests on four sections of the Missouri River during three investigative studies.

[KW-ANOVA H (3, N=95)= 20.01, p=0.02], but small sample sizes precluded post-hoc pairwise comparisons.

Dive success did not differ among the River (4/9, 44.4%) Canyon Ferry (5/6, 83.3%) and Hauser (2/7, 28.6%) (Z-test of two proportions, all p-values > 0.05). Dive success was lower on Holter (0/9, 0%) when compared to Canyon Ferry (Z-test of two proportions, z=3.35, p=0.001). Mean length of fish delivered by River birds to nests, were significantly smaller than those delivered on Holter (LSD test t = 13.25, p = 0.004; Table 2). Sample sizes precluded significance during pairwise post-hoc comparisons

Table 2. Foraging success of male osprey on four sections of the Upper Missouri River, Montana, 1998-1999.

River Section	Hours Monitored	Dive Success[1] N (%)	Deliveries Total	Deliveries Rate[2]	Prey Length (cm) Mean (SE)	Prey Length (cm) Est. Mean Mass (g)
River	156	4/9 (44.4)	49	0.31	24.8 (11.4)	303.9
Canyon Ferry	104	5/6 (83.3)	21	0.20	31.2 (11.4)	523.6
Hauser	90	2/7 (28.6)	29	0.32	28.6 (10.7)	391.1
Holter	101	0/9 (00.0)	27	0.27	33.7 (12.9)	706.4

Dive Succes[1] = Successful deliveries/number of attempts. Dive success only measured during 1999 field season
Rate[2] = Deliveries per hour

between the River and Canyon Ferry (LSD test, t = 12.33, p= 0.03; Table 2).

I identified 220 opercle, 66 cleithra, and 9 pharyngeal teeth were from prey remains collected below occupied osprey nests. Bones gathered and separated by section of river revealed a dominance of suckers (Figure 8). Deliveries made to nests during 1998 and 1999 showed that the majority of fish captured and taken to nests were suckers (Figure 9).

Suckers also made up the greatest biomass during 1998 and 1999 of gill netting sampling (Figure 10). On Canyon Ferry suckers made up at least 60 % of the biomass caught each year. The number of fish caught per spring floating gill net on Canyon Ferry for 1998 and 1999 combined (22.4) was more than double the amount caught on the other two reservoirs (Hauser = 4.15, Holter = 5.06) (Figure 11).

The number of fish caught in spring floating gill nest on Canyon Ferry did not differ between 1998 and 1999 ($?^2$= 1.29, df=2, p = 0.54) nor did the number of fish delivered to nests ($?^2$= 0.99, df=2, p = 0.61), thus data were pooled across years. After

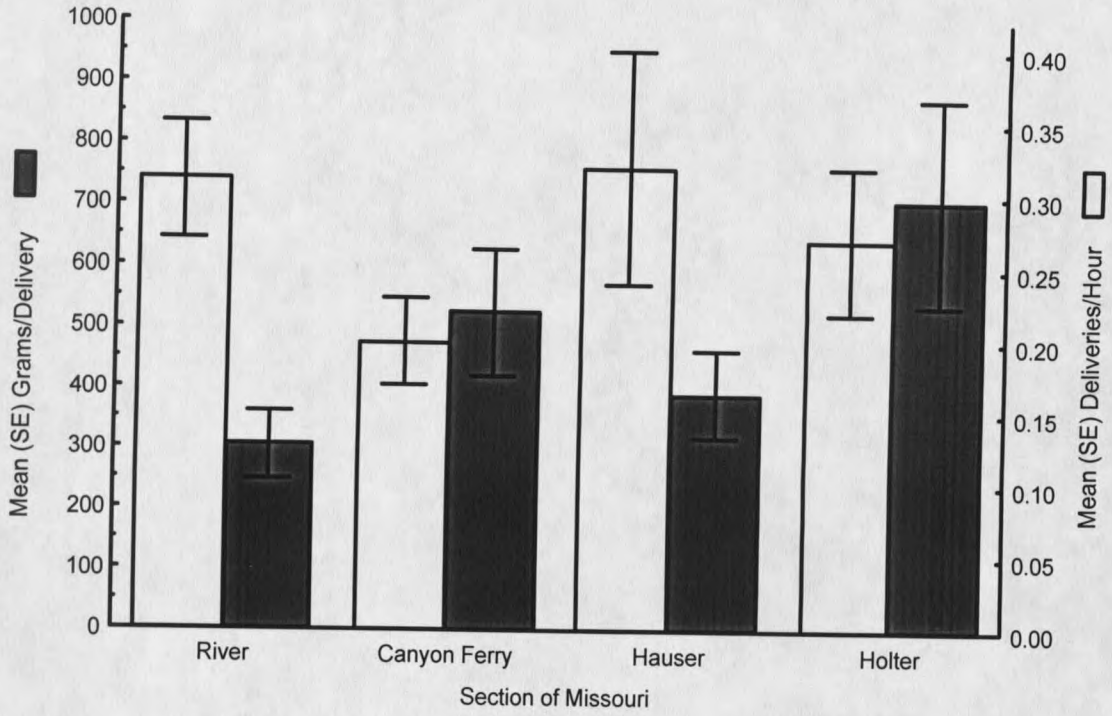


Figure 7. Mean mass of fish delivered to nests and the rate of deliveries per section of the Missouri during 1998 and 1999.

pooling, Canyon Ferry osprey were capturing suckers in greater number than predicted by gill net catches (Z-test of two proportions, $z=-8.95$, $p<0.001$). Conversely, osprey on Canyon Ferry captured fewer trout than predicted (Z-test of two proportions, $z=4.34$, $p<0.001$). The Other category of fish was taken in equal proportion to that expected from netting data by osprey on Canyon Ferry Reservoir (Z-test of two proportions, $z=0.78$, $p=0.22$).

On Hauser reservoir, a significant difference occurred between the number of each category of fish delivered to nests when compared to what was expected from the spring floating gill net catch ($?^2 = 8.83$, $df = 2$, $p < 0.012$). Small sample sizes precluded post-hoc pair wise comparisons of each category (Z-test of two proportions, all p's > 0.035).

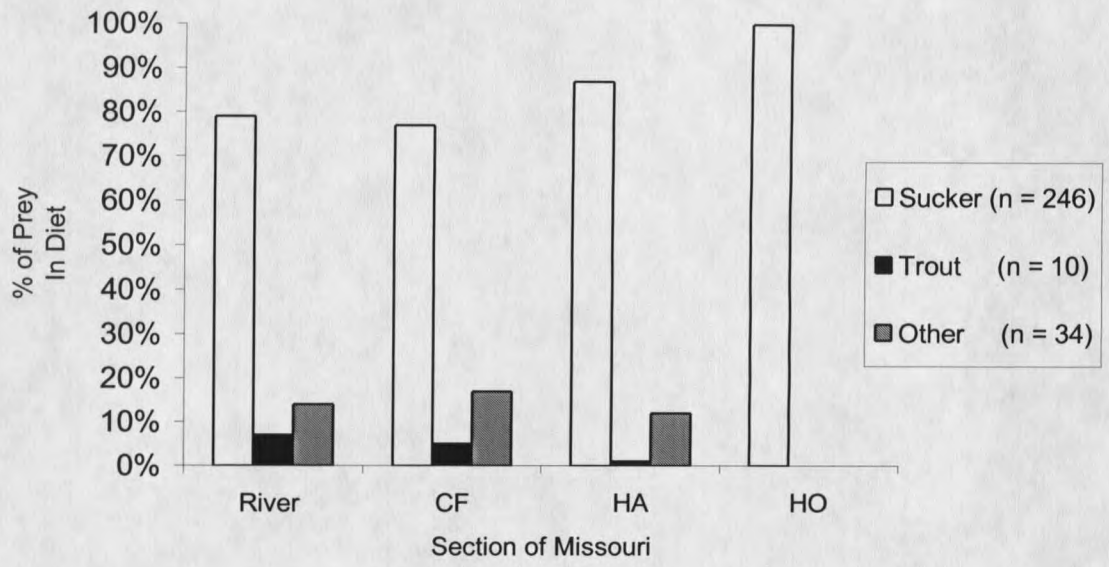


Figure 8. Percent of four families of fishes included in the osprey diet, based on diagnostic bones collected below nests and feeding perches.

Lastly on Holter, suckers were taken in greater proportion by osprey than expected from gill netting data (Z-test of two proportions, $z = 3.55$, $p < 0.001$). Conversely, trout were delivered much less than expected from gill netting data (Z-test of two proportions, $z = -3.39$, $p < 0.001$). The Other category was captured and delivered by osprey in equal proportion to their availability (Z-test of two proportions, $z = -3.91$, $p < 0.001$).

The most commonly caught species of fish differed significantly between the River (Whitefish) and the reservoirs (Suckers) (Table 4 and 5). The species of fish selected by osprey on the River was similar to that selected on the reservoirs. Suckers osprey on the River was similar to that selected on the reservoirs. Suckers were captured and delivered by male osprey in greater proportion than was expected from floating gill nets (Z-test of two proportions, $z = 4.28$, $p < 0.001$). Trout were delivered in equal proportion to their

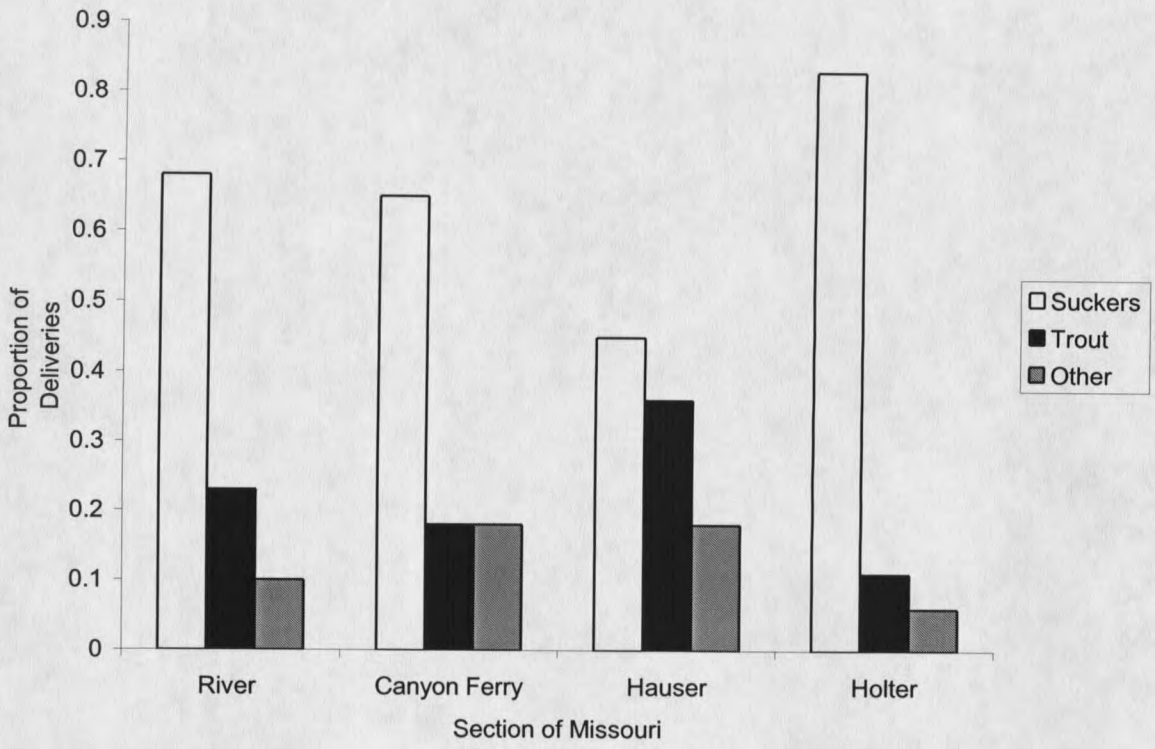


Figure 9. Proportions of prey deliveries by category of fish (Suckers, Trout, and Other) per section of the study area (River, Canyon Ferry Reservoir, Hauser Reservoir, and Holter Reservoir) during years (1998 and 1999) combined.

availability from gill nets (Z-test of two proportions, $z = 0.56$, $p = 0.29$). Conversely, the Other category was delivered less than was expected from spring floating gill netting data (Z-test of two proportions, $z = -4.88$, $p < 0.001$).

Because of low-resolution maps detailing power line distribution, I was unable to perform accurate analyses to determine a change in the number and/or distribution of power lines along my study area. However, power line numbers and distribution was not believed to have changed considerably since the late 1970's and new power lines installed since the mid 1980's have been placed underground and thus are unavailable to nesting osprey (L. Lane and M. Evans, Montana Power Co., pers. Comm.).

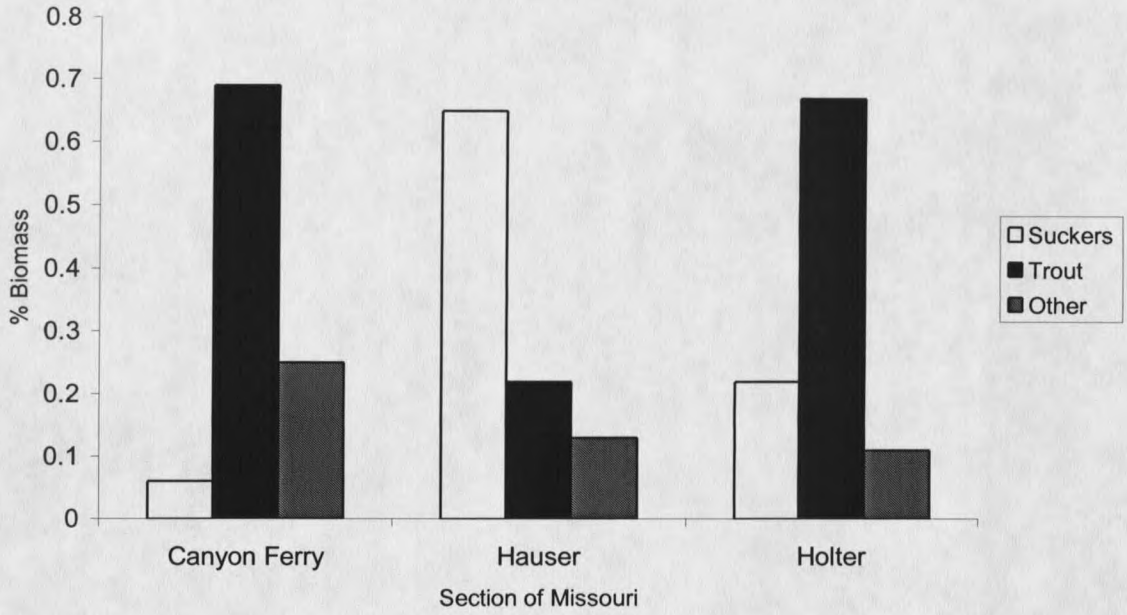


Figure 10. Percent biomass represented by 3 categories of fish in gill net catches on three reservoirs of the Upper Missouri River during the spring of 1998 and 1999 (data combined).

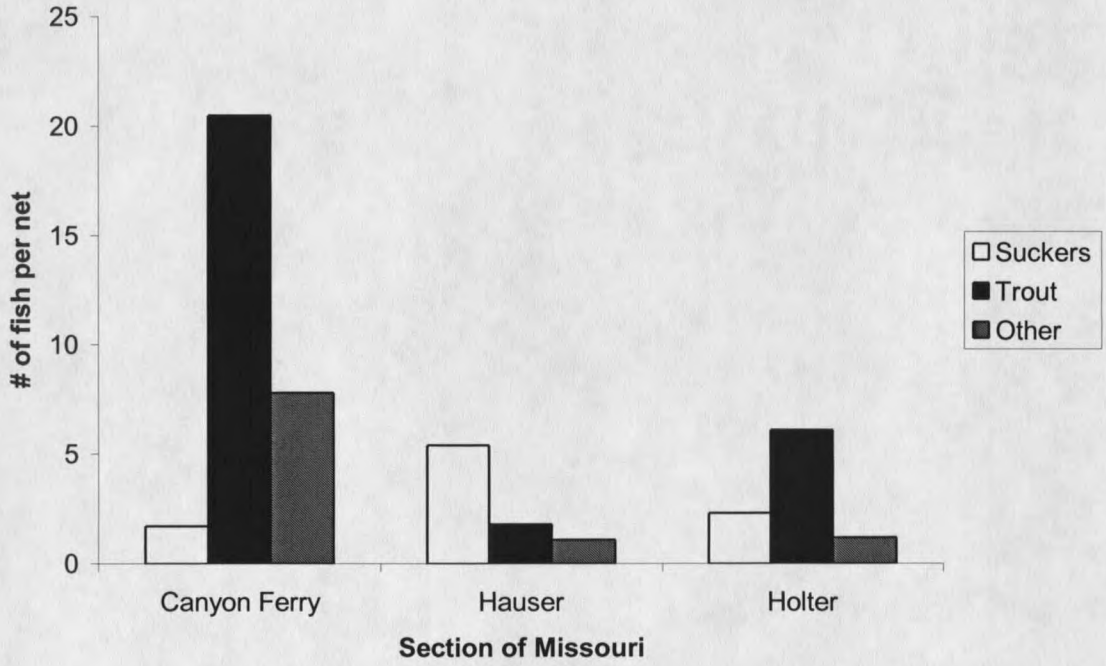


Figure 11. Relative abundances of three classes of fish (number/net) on three reservoirs along the Upper Missouri River during 1998 and 1999 (data combined).

Table 3. The number of each fish species electroshocked on the River section below Toston Dam during the spring of 1998 and 1999.

Species	Distance (miles)		Shock Time(hours)		Total Fish Encountered		Fish/km	
	1998-99	1999[1]	1998-99	1999[1]	1998-99	1999[1]	1998-99	1999[1]
Suckers[1]	7.75	1.75	299	138	522	171	67.35	13.73
Brown Trout	7.75	1.75	299	138	96	34	12.39	2.73
Rainbow Trout	7.75	1.75	299	138	147	135	18.97	10.81
Carp	7.75	1.75	299	138	369	72	47.61	5.77
White-fish	7.75	1.75	299	138	842	694	108.66	55.65

Suckers[1]-Combined White and Longnose Suckers.
1999[1] – Shocking data was combined across years except for an additional shocking sampling run which occurred in 1999.

Table 4. The number of each fish species electroshocked on the River section above Toston Dam during the spring of 1998 and 1999.

Species	Distance(km) 1998-99	Shock Time(min.) 1998-99	Total # Fish Captured 1998-99	Fish/km 1998-99
Suckers[1]	27.36	308	664	24.27
Brown Trout	27.36	308	236	8.63
Rainbow Trout	27.36	308	124	4.53
Carp	27.36	308	25	0.91
Whitefish	27.36	308	755	27.59

Suckers[1]-Combined White and Longnose Suckers

DISCUSSION

The density of occupied nests on all sections of the study area increased from Grover's (1984) initial investigation in 1981-82. Increases were most significant on the River and Hauser reservoir, which changed the nesting distribution of osprey along the Upper Missouri River. The average number of fledgling osprey produced did not differ across any section of the study area. This evidence supported the prediction of the IFD that fitness would be equal across patches of habitat of differing quality. Therefore, the first two IFD requirements stated in the Introduction were satisfied: 2) The population's nesting distribution changes in response to an increased density of individuals and 4) Fitness must be equal across patches. Although my estimate of fitness was equal across sections, my estimate of intake (delivery rates) differed across study area sections. This finding contradicted the equal intake across patches prediction of the IFD and indicated that osprey on the Upper Missouri River may not be distributing themselves in an ideal manner.

IFD predictions and osprey on the Upper Missouri River

Habitat Quality

Cuthbert and Rothstein (1988) discovered that one factor most influencing the distribution of osprey in Voyageurs National Park was the number and diversity of fish contained in a body of water needed to large. Thus, when the reservoirs on my study

area were ranked by the total number of fish caught in spring floating gill nets, the following order resulted from highest to lowest quality: Canyon Ferry, Hauser, and Holter. Similarly, the same order resulted when the reservoirs were ranked in order according to the number of pairs found on each section.

Direct comparisons of quality between the River and the reservoirs could not be made because different sampling methods were used to estimate fish numbers. Previous investigations suggested that the River was of lower quality than the reservoirs due to the rapid current, riffles, and variable water levels (Grover 1984; Restani and Harmata 1992). Rapid current and riffles are believed to increase turbidity and to reduce clarity of the water, thereby making it difficult for hovering osprey to observe fish (Grubb 1977, Stinson 1978, Flook and Forbes 1983, Swenson 1981, Vana-Miller 1987, Machmer and Ydenberg 1990). High water levels are also believed to reduce the foraging efficiency of osprey because the number of shallow pools decrease, making prey detection and capture increasingly difficult (Koplin et al. 1977; MacCarter and MacCarter 1979; Van Daele and Van Daele 1982). As a result, the River section was determined to be the lowest quality section in terms of prey accessibility and potential availability.

Productivity

The mean number of young produced on each section of the study area was similar, supporting another prediction of the IFD. Since overall productivity of the birds residing and foraging on my study area was equal and the quality of each section differed in total number of fish caught, characteristics of nestlings were examined to determine if the quality suggested by prey availability was manifested in characteristics of

young osprey. Studies have shown that birds in lower quality habitat have displayed smaller biometric measurements than birds in higher quality habitats (Lack 1971; Grant 1979). For example, Steeger et al. (1992) found that osprey on lower quality habitat grew slower and fledged at lower weights than birds on higher quality habitat.

The patch quality suggested by fish numbers was not expressed in nestling condition on my study area. I discovered that the condition of nestling osprey was not different across sections of my study area. McLean (1991) found that the asymptotic weight of nestling ospreys, the average growth rate, and the fledging age of nestlings were the same between two studies, while prey availability had changed dramatically.

The lack of difference observed between the sections of my study area might be due to the small sample sizes I obtained within sections. Lastly, the total number of fish captured by adult male osprey or in gill nets on each section may not be a true indication of the quality of each habitat, but the more plausible explanation is that prey is not a limiting factor on the Upper Missouri River. Forbes and Ydenberg (1992) hypothesized that very different feeding situations may not affect breeding success if osprey adopt a conservative breeding strategy to buffer their food-delivery ability against unpredictable but potentially devastating events. Thus, the sections along the Upper Missouri River may differ in quality but birds on the lower quality habitats may still be able to capture enough food to produce and raise the same number of birds as the higher quality habitats.

Foraging

Prey delivery rates differed by section. Canyon Ferry birds delivered fewer prey per hour than did River birds, contradictory to the predictions of the IFD. But Canyon Ferry adult male osprey delivered larger fish, compensating for the lower number of deliveries. River birds, on the other hand, delivered smaller fish but compensated for it with a higher rate of delivery. Differing delivery rates across sections of habitat have been discovered in numerous studies regarding tests of the IFD (Monaghan 1980; Sutherland 1982; Sibly and McCleery 1983; Goss-Custard et al. 1984). These studies found that the average intake was usually much higher on the higher quality sites. I, on the other hand, found that the lowest average delivery rate occurred on the highest quality section, Canyon Ferry.

On my study area, birds on the highest quality habitat brought significantly larger fish to nests than birds on the lowest quality habitat. Studies have shown that osprey do exhibit differences in foraging behavior based on the quality of habitat on which they forage and/or reside. Steeger et al. (1992) discovered that significantly larger fish were delivered on the Nelson arm of Kootenay Lake in British Columbia, as opposed to the Creston Valley of Kootenay Lake. Nelson was considered the higher quality of the two areas based on the size of fish captured and the lower amount of energy birds on the Nelson arm exerted in catching prey. But, no difference was found in the breeding performances of both areas. Thus, Canyon Ferry and Nelson may be similar due to the larger fish caught on each and the equal reproductive performances across the respective populations.

Canyon Ferry osprey seemed to exert less energy than birds on the other sections of the study area just in terms of dive success, but small sample sizes reduced the strength of the inferences I could make. Analysis of energy exertion in regards to flapping flight, soaring, and time away from nests did not reveal significant differences among sections. The fact that time away from the nest was not different between sections of study area does not rule out the IFD as a predictor of osprey distribution on the Upper Missouri River. Petit and Petit (1996) found that prothonotary warblers which resided on a patch of habitat which they determined as the higher quality, actually spent more time away from the nest area but less time foraging. Osprey on the Canyon Ferry may utilize a similar kind of activity budget over the course of the day, thus equaling the amount of time birds on lower quality habitats spent away from the nest. Steeger et al. (1992) found that osprey on better quality habitats expended less energy flying and foraging than osprey on the lower quality habitat, thus larger sample sizes in regards to the amount of energy exerted might reveal differences which correlate with differences in section quality.

The dive success of male osprey was also examined as a further measure of effort that might explain the difference observed in delivery rates across sections of the study area. The number and percent of dives that were successful was also calculated but small sample sizes limit extrapolation and interpretation. Steeger et al. (1992) discovered that on 2 different sections of Kootenay Lake, osprey on the higher quality section were 13% more successful than osprey on the lower quality section. Thus, power analysis was performed on all sections of my study area to determine the sample size needed to detect

a difference in dive success of 13 %. The section with the largest sample size (n=9) needed a sample size of 249 to determine a difference in dive success of 13%. Thus, the indication is that larger sample sizes are needed to definitively determine a difference between sections in dive success.

Prey are probably not limiting on the study area, so osprey may be distributing themselves in relation to nest site availability. Studies have shown that when birds are not limited by prey, nest site availability can predict distributions just as effectively as food availability (Newton 1979; Village 1983; Diaz et al. 1998). For osprey, observations indicate that populations have been limited by nest site availability in a number of instances (Postupalsky 1971, Mace et al. 1987, Ewins 1997). Further evidence for nest site availability limiting osprey populations is indicated by the fact that the species reacts favorably to the construction of artificial nest sites (Poole 1989, Gieck et al. 1992, Ewins 1994, Ewins 1996, Ewins and Miller 1995). In all cases, after the construction of artificial nest sites took place, the population increased indicating that birds could not obtain suitable nesting areas on traditional nest substrates. Contradictory to this evidence, I found empty nest sites on all sections indicating that nest site availability is probably not limiting. This may suggest that nest site availability and prey availability may be working in concert to drive the change in nesting distribution I observed.

CONCLUSIONS

Differences in delivery rates contradict predictions of the IFD theory, yet productivity and preliminary analysis of dive success and the change in the distribution of nesting osprey over time, support the IFD as a predictor of osprey distribution along the Upper Missouri River. Also delivery rates taken in the context of the sizes of fish delivered may conform to the predictions as well.

The assumptions of the IFD are hard to conform to in real world settings and most likely the assumptions of equal competitive abilities, continuous input system, as well as the ideal assumption, may have been violated. Milinski (1984) and Sutherland and Parker (1985) both indicated that differences in competitive abilities does not necessarily produce departures from IFD predictions. Thus, the competitive abilities assumption may not apply and as indicated above, the predictions seem to have been validated at least from preliminary investigation. Additionally, Milinski (1988) indicated that the IFD was robust to violations of its assumptions since numerous studies have validated and confirmed repeatedly the IFD's predictions while violating at least one of it's assumptions.

The patches I have defined may not indicate the true patches of habitat which osprey are governed. Tyler and Hargrove (1997) indicated that the scale at which the IFD is applied to a landscape is very important. They recommended that the extent of the area over which the IFD should be used should be similar to the maximum daily movement distances of the animals under study. Thus, patch designation taking into consideration

maximum daily movement of birds on the study area, may produce a better fit to IFD predictions by osprey on the Upper Missouri River.

The fitness currency I focused on for my study, average number of fledglings produced, may not have been the correct measure of fitness. It has been shown that raptor population levels are more sensitive to adult and sub-adult mortality rates than they are to reproductive levels (Grier 1980; Nichols et al. 1980). If this is true in reference to osprey populations, then further investigation of fledgling mortality and survival needs to be conducted.

Selection pressures may be acting on osprey nesting on the Upper Missouri River and forcing them to maximize their long-term or lifetime fitness, instead of the number of young produced within a given year. Investigation over a longer period of time may indicate more complete adherence to the IFD predictions for osprey. All in all, proper designation of fitness currency, a longer study, and incorporating phenotype limited IFD theory and predictions may reveal that osprey do distribute themselves in a manner predicted by IFD theory.

MANAGEMENT IMPLICATIONS

If in fact the IFD is an adequate predictor of how osprey will distribute themselves across patches of habitat, then the implications for osprey management are significant. The IFD could be used to determine the affects of habitat loss on osprey populations. For example in Montana, if hydroelectric dams were suddenly removed, the IFD could predict how the reduced nesting habitat and prey availability would affect how osprey distributed

themselves across a landscape. Additionally, if the IFD accurately predicts osprey distributions, then the model would demonstrate the habitat variables most likely affecting osprey habitat selection, allowing managers to manipulate landscapes either to attract or repel osprey. If managers know through the IFD which habitat variables most likely affect a species, then they will know what annual conditions (weather or human) might affect survival, habitat use, and distribution. Lastly, in the case of osprey, managers can also determine what patches of habitat will be occupied first when new areas of suitable habitat are created (i.e., when a new dam is constructed).

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