Settlement patterns, foraging behavior, and reproductive success of ospreys along a heterogeneous riverine corridor

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Abstract: In 1998 and 1999, we determined the spatial distribution, foraging behavior, and reproductive success of ospreys (Pandion haliaetus (L., 1758)) nesting along the upper Missouri River, Montana. We combined our data with that collected in the same area in 1981–1982 and 1990–1991 to investigate factors influencing settlement patterns. The study area was composed of four distinct habitats, three reservoirs and one free-flowing river section. Although number of occupied nests on each habitat increased from 1981–1982 to 1998–1999, the greatest percentage increases in nest density occurred on habitats previously hypothesized to contain the least prey. Osprey reproductive success was positively related to foraging rates, which differed across habitats, being highest on reservoirs and lowest on the free-flowing river. However, reproductive success was adequate for replacement on each habitat. Most fish consumed by ospreys on each habitat were suckers (Catostomidae), followed by salmonids and cyprinids. Fish density, determined from gill netting, was highest on the largest and shallowest reservoir. Over two decades, ospreys shifted their relative spatial use of the upper Missouri River such that reservoirs were occupied first and the free-flowing river section was occupied last. The degree to which presence of conspecifics, distribution of nest trees and prey, and dispersal affected settlement patterns probably varied by spatial scale.

Résumé : En 1998 et 1999, nous avons déterminé la répartition spatiale, le comportement de recherche de nourriture et le succès reproductif chez des balbuzards pêcheurs (Pandion haliaetus (L., 1758)) qui nichent le long du cours supérieur de la Missouri, Montana. Nous avons combiné nos données avec d’autres récoltées dans la même région en 1981–1982 et en 1990–1991 afin d’étudier les facteurs déterminants des patrons de colonisation. La région d’étude comprend quatre habitats distincts, trois réservoirs et une section de rivière à écoulement libre. Bien que le nombre de nids occupés ait augmenté dans chacun des habitats de 1981–1982 à 1998–1999, l’accroissement le plus important de densité des nids s’est fait dans des habitats considérés antérieurement comme contenant le moins de proies. Le succès de la reproduction chez ces balbuzards pêcheurs est en relation positive avec les taux de recherche de nourriture qui diffèrent d’un habitat à l’autre, atteignant un maximum dans les réservoirs et un minimum dans le cours de rivière libre. Cependant, le succès reproductif est suffisant pour permettre le remplacement dans tous les habitats. Les poissons les plus consommés par les balbuzards pêcheurs dans tous les habitats sont les catostomes (Catostomidae), suivis des salmonidés et des cyprinidés. La densité des poissons, déterminée à l’aide de filets maillants, est maximale dans le réservoir le plus grand et le moins profond. Au cours des deux décennies, les balbuzards pêcheurs ont modifié leur utilisation relative de l’espace dans le cours supérieur de la Missouri de telle façon que les réservoirs sont colonisés les premiers et la section de rivière libre la dernière. L’importance de la variation des patrons de colonisation due à la présence d’autres balbuzards pêcheurs, à la répartition des arbres de nidification et des proies et à la dispersion change probablement en fonction des échelles spatiales.

[Traduit par la Rédaction]

Introduction

The distribution of individuals varies across landscapes containing habitat patches of differing quality, and habitat selection with its associated demographic consequences has important implications for population ecology, evolution, and conservation. Prominent theories of habitat selection propose that settling individuals either avoid or seek conspecics or select the best unoccupied habitat (e.g., Brown 1969; Fretwell and Lucas 1970; Rosenzweig 1985; Stamps 1988; Pulliam and Danielson 1991). Studies of avian habitat use patterns and selection processes have focused on short-lived species because investigating changes in settlement behaviors and spatial distribution of long-lived species requires decades of research effort. Notable exceptions include a 32-year study of imperial eagles (Aquila adalberti Brehm, 1861) (Ferrer and Donazar 1996) and an 11-year study of black kites (Milvus migrans (Boddaert, 1783)) (Sergio et al. 2003b), both of which showed that settling individuals in increasing populations responded to habitat heterogeneity, which in turn affected fitness.

Osprey (Pandion haliaetus (L., 1758)) populations worldwide have increased after recovering from exposure to environmental contaminants during the 1940s to the 1970s. Recovering populations have exploited habitat created dur-
ing reservoir construction and the placement of utility poles and other artificial nest structures (Henny and Kaiser 1996; Ewins 1997). These increasing populations of ospreys have provided another opportunity to examine settlement patterns and selection over long temporal and large spatial scales. For example, in Estonia the overall productivity of a nesting population declined over 15 years in response to the establishment of new breeding territories (Lõhmus 2001). New pairs settled into habitat farther from lakeshores and produced fewer young than established pairs who occupied sites along shorelines. Therefore, habitat selection of a subset of breeders, not density dependence, where all pairs had lowered reproductive success, decreased overall population productivity. The generality of this finding remains unknown.

The spatial distribution, reproductive success, and diet of ospreys in central Montana were determined along nearly 200 km of the upper Missouri River in 1981 and 1982 (Grover 1984). This stretch of river contains three reservoirs (Canyon Ferry, Hauser, and Holter) and one swift-flowing reach (the River). Reservoir and river habitats varied in quality, with ospreys nesting at greater density and fledging more young per nest on Canyon Ferry and Holter reservoirs than on Hauser Reservoir and the River. Diet varied among the reaches and differences in prey availability and abundance, neither of which were quantified, were hypothesized to account for osprey distribution and reproduction. None of the subpopulations were limited by the availability of nest sites (Grover 1983), a common characteristic of the species because of its willingness to nest on utility poles and artificial nest structures (Poole 1989; Ewins 1996; Henny and Kaiser 1996).

The same four habitats of the upper Missouri River were resurveyed in 1990 and 1991 (Restani and Harmata 1992). Number of occupied nests along the entire study area had increased from 83 to 100 during the 10-year period, with the most significant increases occurring on the River and Hauser Reservoir, areas originally hypothesized to contain the least prey (Grover 1984). Based on the growth of the population and the pattern of settlement, it appeared that Canyon Ferry and Holter reservoirs continued to represent the highest quality habitat and had possibly reached carrying capacity by the early 1990s. Neither reproductive success nor foraging rates were quantified in the 1990–1991 study.

We believed that the osprey population along the riverine corridor would continue to increase during the 1990s and we saw an opportunity to combine previously collected data with new information to place settlement patterns over nearly 20 years within a habitat selection framework. In 1998 and 1999, we determined osprey spatial distribution, foraging behavior, and reproductive success along the same study area surveyed in 1981–1982 and 1990–1991. In contrast to earlier studies, we also determined prey distribution and abundance. We tested the hypothesis that Canyon Ferry and Holter reservoirs represented high-quality habitat and Hauser Reservoir and the River represented poor-quality habitat. Based on osprey habitat use in the earlier studies, we also predicted that prey abundance and foraging rates would be higher on Canyon Ferry and Holter reservoirs than on Hauser Reservoir and the River. We assumed that nest sites were not limiting because an abundance of utility poles and trees containing old unoccupied nests occurred between occupied territories on each study area section.

Methods

The study area extended 191 km along the upper Missouri River from Three Forks to Wolf Creek, Montana, and included 1.6 km of shoreline on each side of the river. Four dams (Toston, Canyon Ferry, Hauser, and Holter) created four reservoirs of similar name moving downriver from Three Forks. Following the methods of previous studies, we designated four study area sections: the River and Canyon Ferry, Hauser, and Holter reservoirs (Grover 1984; Restani and Harmata 1992). Toston Dam withheld little capacity and Toston Reservoir fluctuated greatly in response to discharge (Montana Fish, Wildlife and Parks 1992); thus, we included this “reservoir” within the River section because it had characteristics that made it more similar to a free-flowing river (e.g., riffles, rapids, exposed boulders, gravel bars) than to the three large reservoirs, which were distinguished by large expanses of flat, slow-moving water. Canyon Ferry Reservoir experienced severe fluctuations in water level, but its size (approximately 200 km²) ensured it retained characteristics of a lake. Hauser and Holter reservoirs had stable water levels.

We defined osprey habitat as the sum total of characteristics of an area (e.g., prey, nest substrates) that produced occupancy (Johnson 1980; Hall et al. 1997; Jones 2001). Nesting habitat use (i.e., pattern) reflected habitat selection, the hierarchical decision-making process of settlement, which we equated with the distribution of osprey nests along the four study area sections. Habitat quality of the four sections was ranked based on osprey reproductive variables, not nesting density (Van Horne 1983; Hall et al. 1997), and varied along a continuum from poor to high (Grover 1984).

On the study area, fish populations were dominated by Cyprinidae (carp, *Cyprinus carpio* (L., 1758)), Catostomidae (white sucker, *Catostomus commersoni* (Lacepède, 1803), and longnose sucker, *C. catostomus* (Forster, 1773)), Salmonidae (rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792), brown trout, *Salmo trutta* L., 1758, and mountain whitefish, *Prosopium williamsoni* (Girard, 1856)), and Percidae (yellow perch, *Perca flavescens* (Mitchill, 1814)). Low-elevation (1350 m) riparian vegetation was composed of willow (*Salix* spp.) and cottonwood (*Populus* spp.). Flood plains were covered with grasses (*Agropyron* and *Poa* spp.) and sagebrush (*Artemisia* spp.). A mixture of grassland, sagebrush, and juniper (*Juniperus* spp.) covered gently rolling hills. Higher elevation (2000 m) slopes were dominated by coniferous trees, mostly ponderosa pine (*Pinus ponderosa* (Engelm.)) and Douglas-fir (*Pseudotsuga menziesii* (Beissn.)). Power poles and nest platforms provided ospreys ample opportunity to nest on human-made structures. Land use on the study area included farming, cattle grazing, forestry, and mining. Recreational use of the reservoirs for fishing and pleasure boating was high. Climate was semiarid with annual precipitation averaging approximately 30 cm.

We conducted fieldwork from early May through August in 1998 and 1999. We determined early- and late-season
nest site occupancy and productivity during four aerial surveys (8 May and 25 July 1998 and 8 May and 28 July 1999). An occupied nest possessed at least one of the following characteristics: young were raised, eggs were laid, one adult was observed sitting low on the nest, presumably incubating, or two adults were present on or near the nest (Steenhof 1987). We used a global positioning system to plot nests on 1:100 000 scale maps. We used these maps to determine length of shoreline (km) available to nesting ospreys on each study area section to estimate breeding density (number of occupied nests per kilometre). From the ground, we visited each nest multiple times throughout the breeding season to corroborate occupancy and productivity observations made from aircraft (Ewins and Miller 1995). We used young of advanced age (within 1 week of fledging) as our productivity estimate (Grover 1984). We ranked the relative habitat quality of each study area section by multiplying mean number of young fledged per occupied nest by number of occupied nests per kilometre to estimate number of young produced per kilometre.

We determined prey delivery rates of adult male osprey with young by conducting nest watches on each study area section from 18 June to 11 August 1998 and from 18 June to 5 August 1999. Sections were numbered one through four; the section monitored first each year was selected randomly and successive sections were monitored in sequence. We also randomly selected individual nests within sections. We observed nests in 4 h time periods from 0500 to 2100 MDT to obtain a representative sample of foraging activity across all daylight hours. A study area section was completed only after osprey nests had been observed in all time periods between 0500 and 2100. This cycle was completed 2–4 times per year. We did not conduct nest watches in rain or when wind was >45 km/h (Poole 1982).

We positioned a vehicle or boat within 90 m of nests and used a 40-power spotting scope to observe prey deliveries. We recorded time of delivery, fish species, and fish length (cm) in reference to osprey body length (Eriksson 1986; Machmer and Ydenberg 1990; Carss and Godfrey 1996). We had difficulty distinguishing between white and longnose suckers and between brown and rainbow trout, so we combined these species into “sucker” and “trout” categories, respectively. An “other” category included less commonly captured fish, such as yellow perch, mountain whitefish, kokanee (Oncorhynchus nerka (Walbaum, 1792)), walleye (Sander vitreus (Mitchell, 1818)), Utah chub (Gila atraria (Girard, 1856)), and carp.

We used linear regressions between lengths and masses of different fish species measured during electrofishing and gill netting (see below) from each study area section to estimate mass (g) of fish delivered to nests. Estimates of slope and intercept resulting from regression equations were incorporated into the equation $\log_{10} y = a + b \log_{10} x$ for each species (Anderson and Neumann 1996), where $y$ is mass (g) and $x$ is length (cm).

From nest observation data we calculated mean delivery rate (deliveries per day) and mean delivery amount (grams per delivery). We estimated mass of fish brought to nests each day by multiplying deliveries per day by grams per delivery by 16 h per day, the length of daylight during summer. We did not standardize delivery rates (i.e., number of deliveries per day) to individual nests by brood size because male ospreys do not adjust foraging rates by brood size (Stinson 1978; Poole 1982; Eriksson 1986). However, to compare nestling consumption rates among the different study area sections, it was necessary to divide mass of fish brought to nests per day by the average brood size of successful nests for each study area section.

We collected prey remains under nests at the conclusion of each nest observation period to supplement diet information obtained during prey delivery observations (Grover 1984). Prey remains were also collected at the end of each breeding season from nests where we were unable to conduct nest watches because of obstructive terrain or vegetation. Identification to species and number of individual prey were determined using a reference collection of diagnostic bones (opercles, cleithra, and pharyngeal teeth).

Montana Fish, Wildlife and Parks fisheries biologists provided us May 1998 and 1999 floating gill netting data from the three reservoirs and electroshocking data from the River. We determined prey species composition and abundance from these data. The River section was sampled by electroshocking because it was too shallow and swift to sample with gill nets, which prevented us from comparing abundance of prey between the reservoirs and the River.

Fisheries biologists set 15 nets per year on Canyon Ferry Reservoir for one night in early May 1998 and 1999. Nets were distributed along the upper, middle, and lower reaches of the reservoir. The same general protocol for net placement was used on Hauser and Holter reservoirs, but dates and number of nets varied (10 nets per year from 18 to 21 May and 8 nets per year from 24 to 28 May, respectively). We calculated mean (SE) number of fish captured per net for each reservoir. Fisheries biologists electroshocked both shorelines of the River section each spring (9 June 1998 and 12 May, 20 May, and 21 May 1999). Biologists recorded only the total number of fish shocked per shoreline, thus we were unable to present variability about the mean point estimate of fish per kilometre.

We pooled yearly data from each study (1981–1982 (Grover 1983, 1984), 1990–1991 (Restani and Harmata 1992), and 1998–1999 (this study)). Statistical analyses for the 1998–1999 data were conducted with SPSS® Version 13.0 (SPSS Inc., Chicago) and unless indicated otherwise, results are means ± SE. We limited the number of statistical tests to a priori hypotheses to avoid data dredging and the reporting of spurious findings (Johnson 1999; Anderson et al. 2001). We used one-way ANOVA and Tukey post hoc tests to determine whether differences in osprey foraging behavior and prey abundance existed among study area sections. Data were log-transformed prior to analyses to improve normality (Kolmogorov–Smirnov test). Homogeneity of variances was examined with Levene’s test.

**Results**

We located 156 occupied territories from 1998 to 1999. The mean number of occupied nests on each section of the study area increased from 1981–1982 to 1998–1999 (Fig. 1). The greatest percentage increases in nest density (pairs per kilometre) occurred on the River (88%) and Hauser Reservoir (80%), with moderate increases observed on Holter
(20%) and Canyon Ferry (17%) reservoirs. In 1981 and 1982, the most young per kilometre were produced on Canyon Ferry Reservoir, followed by Holter and Hauser reservoirs and the River (Table 1). Productivity increased on each study area section from 1981–1982 to 1998–1999. From 1981 to 1982, 100% of nests with eggs or young failed on the River \((n = 4\) failures), compared with 33% on Holter Reservoir \((n = 7)\), 25% on Canyon Ferry Reservoir \((n = 13)\), and 0% on Hauser Reservoir \((n = 0)\). In 1998–1999, 46% of nests with eggs or young failed on the River \((n = 17\) failures), compared with 32% on Canyon Ferry \((n = 20)\) and Hauser \((n = 10)\) reservoirs and 27% on Holter Reservoir \((n = 7)\).

Over the two decades of study, osprey use of natural nest substrates declined and use of artificial structures, such as power poles and nest platforms, increased. Of 83 nests found from 1981 to 1982, 69% occurred on trees, 26% on artificial structures, and 5% on cliffs. Of 51 nests found in 1991, 49% occurred on trees, 45% on artificial structures, and 6% on cliffs. In 1998–1999, of 156 nests found, 70% occurred on artificial structures, 26% on trees, and 6% on cliffs. Unoccupied artificial nest structures and trees containing old nests existed between occupied territories on each study area section during all three survey periods.

We combined number of prey identified from remains \((n = 72)\) and nest watches \((n = 86)\) to determine diet composition. The majority of fish consumed by ospreys on each study area section were suckers \((\text{Catostomidae})\), followed by salmonids and cyprinids (Fig. 2). The “other” category of fish amounted to only 5%–9% \((n = 11)\) of the total sample and was not included in analyses.

Ospreys nesting on Canyon Ferry Reservoir had the lowest prey delivery rates, followed by those on Holter Reservoir, Hauser Reservoir, and the River \((F_{[3,110]} = 2.86, P = 0.040)\) (Fig. 3). On a per delivery basis, ospreys nesting on the River delivered fish of low mass to nestlings compared with ospreys nesting on Canyon Ferry and Holter reservoirs \((F_{[3,91]} = 4.10, P = 0.009)\). Ospreys nesting on the River delivered the least biomass of prey to nests each day \((888 \text{ g})\), followed by those nesting on Canyon Ferry \((1032 \text{ g})\), Hauser \((1152 \text{ g})\), and Holter reservoirs \((1512 \text{ g})\). These amounts were divided by average brood size per successful nest to estimate the number of grams delivered to each nestling by study area section: River, 433 g per nestling per day; Canyon Ferry, 521 g; Hauser, 603 g; and Holter, 822 g. River nestlings received 48% less food per day than Holter Reservoir nestlings.

Because sample sizes were small, we combined data of foraging success from 1981–1982 (Grover 1983) and 1998–1999. Ospreys foraging on Canyon Ferry Reservoir had the highest dive success \((11 \text{ of 17 dives successful, } 65\%)\), followed by 44% dive success on both Holter Reservoir \((17/39)\) and the River \((4/9)\) and 29% success on Hauser Reservoir \((2/7)\). In 1998–1999, the average time ospreys spent away from nests between prey deliveries did not differ among study area sections \((F_{[3,65]} = 0.349, P = 0.790)\). Mean time away from nests ranged from 103 (13) min on the River to 123 (14) min on Holter Reservoir. In 1981–1982, mean time away from nests also did not differ by study area section, ranging from 32 min to 55 min.

Fisheries biologists in 1998 and 1999 set a total of 30 floating gill nets on Canyon Ferry Reservoir and captured 436 fish, mostly salmonids (Fig. 4). On Hauser Reservoir, 20 nets caught 83 fish, mostly suckers, and on Holter Reservoir 16 nets caught 72 fish, mostly salmonids. Overall, Canyon Ferry Reservoir had higher fish density (fish per net) than Holter Reservoir, which had higher fish density than Hauser Reservoir \((F_{[2,63]} = 32.117, P < 0.001)\). Species composition of netted fish differed among reservoirs. Fisheries biologists in 1998 and 1999 electroshocked for a total of 10 h along 35 km of the River and collected 3680 fish, mostly salmonids (Fig. 4).

**Discussion**

The relative distribution of nesting ospreys among four different habitats along the upper Missouri River changed as the population nearly doubled from 1981 to 1998. The two habitats that had the lowest nest densities and were hypothesized to contain the least prey exhibited the largest increases in the number of occupied nests. Habitats of lowest quality were occupied last and relative habitat quality remained relatively consistent among the four habitats over the 20-year study period. It appeared, therefore, that ospreys either avoided settling near conspecifics or settled in the best unoccupied areas. Nesting habitat availability probably did not limit the number of breeding osprey pairs because utility poles, other artificial nest structures, and trees containing old nests on unoccupied territories existed within each of the four habitats.

Prey abundance appeared to shape distribution and density of breeding ospreys in areas that satisfied prerequisites for nest placement. Among the reservoirs, prey abundance was highest in Canyon Ferry, the habitat supporting the highest density of nesting ospreys. Osprey diets varied by study area section and contained 56%–87% suckers. Diet breadth was greatest on Canyon Ferry and Hauser reservoirs, where ospreys consumed nearly 40% alternative prey, primarily salmonids and carp. Suckers were the most abundant prey only in Hauser Reservoir. Osprey diets on Holter Reservoir and the River were composed of >75% suckers, and on both of these reaches salmonids were the most abundant prey. It
appeared, therefore, that ospreys either sought suckers or encountered them more often than other prey during foraging along shallow water adjacent to shorelines (see also Swenson 1979).

Inferring habitat selection processes from prey abundance indices alone may be misleading because prey availability has also influenced raptor foraging rates (Bechard 1982). Therefore, we augmented prey abundance data with observations of foraging osprey to gain additional insight into the relationship between prey availability and habitat settlement. Osprey provisioning rates were a function of both the number of deliveries per day and the size of fish delivered. For example, although River nestlings received a high number of deliveries per day, they consumed the least amount of food per day among the four study area sections because

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\begin{array}{|c|c|c|c|c|c|c|}
\hline
\text{Study area section} & \text{Mean no. of young per occupied nest} & \text{Mean no. of young per km} & \text{Sample size} & \text{Mean no. of young per occupied nest} & \text{Mean no. of young per km} & \text{Sample size} \\
\hline
\text{River (74 km)} & 0.0 & 0.0 & 4 & 1.1 & 0.3 & 37 \\
\text{Canyon Ferry (48 km)} & 1.2 & 0.6 & 52 & 1.2 & 0.8 & 62 \\
\text{Hauser (26 km)} & 1.0 & 0.1 & 6 & 1.3 & 0.8 & 31 \\
\text{Holter (43 km)} & 1.3 & 0.3 & 11 & 1.4 & 0.4 & 26 \\
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\*Data from Grover (1984).

\[\text{Fig. 2. Composition of osprey diets in four habitats along the upper Missouri River, Montana, 1998–1999. Diet was determined from direct observation (n = 86) and remains (n = 72) collected at nests. Sample sizes: River, n = 43; Canyon Ferry, n = 54; Hauser, n = 38; and Holter, n = 23.}\]

\[\text{Fig. 3. Osprey foraging behavior in four habitats along the upper Missouri River, Montana, 1998–1999. Different letters for similarly colored bars denote significant differences using Tukey’s post hoc tests. Sample sizes (deliveries per hour and grams per delivery): River, n = 39 and 38; Canyon Ferry, n = 27 and 17; Hauser, n = 23 and 22; and Holter, n = 25 and 18.}\]

\[\text{Table 1. Reproductive success of ospreys (Pandion haliaetus) by study area section on the upper Missouri River, Montana, 1981–1982 and 1998–1999.}\]

\[\text{Fig. 4. Abundance and composition of osprey prey in four habitats along the upper Missouri River, Montana. Top panel shows data from gill netting. Different letters (a > b > c) denote significant differences using Tukey’s post hoc tests (fish families combined). Number of nets: Canyon Ferry, n = 30; Hauser, n = 20; and Holter, n = 16. Bottom panel shows data from electroshocking.}\]
their parents caught very small fish. Ospreys nesting on Hauser and Holter reservoirs provided their young the most food per day because they captured many large fish. The type of foraging habitat had consequences for reproductive success because brood size at fledging varied in parallel with the daily amount of food delivered per nestling. However, even the “low” quality habitat of the River probably contributed recruits to the burgeoning osprey population in central Montana because reproductive success during the late 1990s was higher than the 0.80–0.90 young per breeding female estimated to be necessary to keep osprey populations stable in the eastern and central United States (Henny and Wight 1969; Spitzer et al. 1983; Postupalsky 1989). Comparing these replacement estimates with those in Montana was reasonable because they were derived from osprey populations inhabiting a large region of diverse habitats and incorporated adult and juvenile survival and movements. Stark differences in habitat and diets between two populations of ospreys in Canada also had minimal effects on reproductive variables (Steeger et al. 1992).

Ospreys were not individually marked on the upper Missouri River, thus the effect of natal and breeding dispersal on settlement patterns was unknown. For example, did the River subpopulation increase slowest because the River was poor-quality habitat or because it was encountered by few colonists? Ospreys exhibit female-biased natal dispersal, with male dispersal distances averaging only 30 km (Henny 1983; Spitzer et al. 1983; Martell et al. 2002). Our study area extended nearly 200 km and short dispersal distances of males may have affected colonization of the River, which existed on the periphery of the study area and was adjacent to small tributaries occupied by even fewer nesting ospreys. Moreover, relatively low reproductive success of River ospreys may have acted in concert with short dispersal distances of ospreys raised on neighboring Canyon Ferry Reservoir to moderate population growth on the River. In contrast, the Hauser Reservoir subpopulation, which like the River subpopulation had low nesting density in the early 1980s, increased in size quickly during the 1990s. Hauser Reservoir was located between Holter and Canyon Ferry reservoirs and may have received colonists from these two highly productive habitats.

Ospreys in each habitat in 1998–1999 had higher reproductive success than pairs in 1981–1982 despite the 47% population increase on the upper Missouri River; thus, density-dependent factors had not yet moderated reproduction. The steady improvement in reproductive performance suggested that prey abundance and availability had increased over time. In fact, intensive stocking of kokanee during the mid to late 1980s took place in Hauser and Holter reservoirs to provide another fishing opportunity for Montana anglers. Hauser Reservoir gained a regional reputation for high angler success (Montana Fish, Wildlife and Parks 1992), and ospreys may also have benefited from the changing abundance and composition of the local prey base. In addition, environmental contaminants may have depressed osprey reproduction during the early 1980s in Montana because DDE continued to reduce eggshell thickness and negatively affect reproduction along the Columbia River as late as 1998 (Henny et al. 2004).

Conspecifics, nest trees, prey abundance, and dispersal were among some of the variables that shaped settlement patterns of ospreys. Their effects probably varied by spatial scale (Wiens 1989), differing within and across study area habitats. For example, ospreys foraged over relatively large areas away from nests; thus, choice of nesting habitat involved cues at small scales, which were likely distinct from cues used to identify remote foraging sites (see also Orians and Wittenberger 1991; Sergio et al. 2003a). Finally, the four subpopulations increased at different rates and occupied habitats of varying quality, and only by initiating a long-term marking program will it be possible to determine the extent of subpopulation connectivity through natal and breeding dispersal. The movement of individuals between the upper Missouri River population and other populations in Montana also remains unknown.

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