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WINTER FORAGING ECOLOGY OF BALD EAGLES IN ARIZONA[1]

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Abstract. Foraging of Bald Eagles (*Haliaeetus leucocephalus*) was examined in winter of 1990 and 1991 along the Colorado River in Grand Canyon, Arizona. Eagles acquired food by hunting live prey (86.6%), scavenging (7.7%), and interspecific piracy (5.7%). Most (99.2% of 1,313) foraging attempts were for rainbow trout (*Oncorhynchus mykiss*). Most foraging attempts occurred in creek habitat where foraging success for live trout was higher than in river habitat, a behavior that presumably increased food intake. Adults exhibited greater foraging success than immatures regardless of attack method, habitat, or prey abundance. Aerial attacks were more successful in creek habitat, and ground attacks were more successful in river habitat. Methods, success, and geographical and hourly patterns of foraging were dependent on prey abundance between years. Eagles modified their foraging strategies to maximize success in a pattern of dynamic optimization under changing conditions.

Key words: Bald Eagle; Haliaeetus leucocephalus; *winter foraging ecology; Colorado River; optimal foraging.*

INTRODUCTION

Optimal foraging theory predicts that prey exploitation is structured to maximize fitness, with foraging success often used as an estimate of fitness (Charnov 1976, Dunbrack 1979, Fischer 1985, Stephens and Krebs 1986, Morse 1990). Birds making optimal foraging decisions must be capable of evaluating energy content of the prey item, energetic cost of the attempt, and probability of success in different habitats using different attack methods (Dunbrack 1979, Fischer 1985, Maurer 1990). Fluctuations in resource abundance also may influence prey exploitation choices and foraging strategies (Davies and Houston 1981, Ewald 1985, Knight and Skagen 1988).

Several hundred migratory Bald Eagles (*Haliaeetus leucocephalus*) winter in Arizona each year, where they move continually over large distances in search of prey (Grubb et al. 1989). Opportunistic foraging by Bald Eagles (Haywood and Ohmart 1986, Watson et al. 1991) indicates that they face constant choices regarding prey exploitation. If stronger selective pressures are brought to bear against migratory birds in winter, as some argue (Lack 1966, Fretwell 1972), then winter is a key time to examine how choices in prey exploitation influence Bald Eagle foraging ecology.

Here, I evaluate winter foraging ecology of a concentration of Bald Eagles exploiting rainbow trout (*Oncorhynchus mykiss*) recently introduced into the Colorado River in Arizona (Brown et al. 1989). My objectives were to: (1) describe foraging behavior, methods, prey use, and success of the eagle concentration; (2) determine if eagle foraging strategies differed by age; and (3) determine if foraging success was influenced by foraging habitat, attack method, and changing prey abundance.

METHODS

I studied foraging eagles in a 3 km^2 area at the confluence (elev. 850 m) of Nankoweap Creek and the Colorado River in Grand Canyon National Park, northern Arizona. The Colorado River in the study area is up to about 10 m deep and ranges from 40–150 m in width (unpubl. data, Glen Canyon Environmental Studies, U.S. Bureau of Reclamation). Nankoweap Creek is a small tributary up to 2 m wide and averaging 30 cm deep (Brown et al. 1989).

Observations were made from a site 800 m west and 100 m above the confluence. Up to five concurrent observers continuously monitored foraging attempts from 30 min before sunrise to 30 min after sunset, 6 February–20 March 1990 and 23 January–13 March 1991. For each foraging attempt we recorded: date, time, eagle age, habitat, foraging method, attack method, prey status and type, success of attempt, and distance to nearest shore. Disturbance days occurred when human activity took place within 500 m of the confluence. Human disturbances may have interrupted natural foraging patterns, and thus were

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eliminated from the analysis of hourly foraging patterns.

Eagles with a primarily white head and tail were designated adults; all others were immatures (Bortolotti 1984). Foraging habitats were subdivided as creek, river, shore, or isolated pool. Isolated pools were basins of water up to about 2 m in diameter and 30 cm deep left along the river shore due to fluctuating water releases from Glen Canyon Dam 110 km upstream. Prey were classed as alive, moribund or injured, and dead. Foraging methods included: (1) hunting for live prey; (2) scavenging for moribund, injured, or dead prey; and (3) interspecific piracy of prey. I did not examine intraspecific piracy, although it was common during the study. Attack method was classified as a ground attack when eagles walked or jumped onto prey, or reached out with beak or talons to capture prey, from a ground perch; an aerial attack occurred when flapping flight was used to land on prey or to otherwise capture prey. A foraging attempt was successful when prey was secured, although the prey may have been pirated before consumption began. Distance to nearest shore for river foraging attempts was estimated to the nearest m for attempts <10 m from shore and the nearest 10 m for attempts >10 m from shore. Distances to landmark objects along the river shore were measured prior to the study, and later used to calibrate observations of distance to nearest shore.

Differences between years were evaluated in light of changing prey abundance. Prey abundance was high in 1990 and low in 1991 as determined by daily visual estimates of trout abundance (Brown and Stevens, in press). Overall prey abundance was estimated based on numbers of trout in the creek because casual observations of river prey abundance paralleled that estimated in the creek. Water in river, creek, and isolated pool habitats was clear more than 90% of the study period, facilitating prey identification and estimates of prey abundance.

Times of foraging attempts were transformed to minutes after or before local sunrise and tested for uniformity or against other distributions with Kolmogorov-Smirnov tests (Norusis 1986). Patterns of foraging success by age, attack method, habitat, and prey abundance (year) were analyzed using log-linear analysis (Norusis 1986). The following were analyzed with χ^2 goodness-of-fit tests: success by foraging method and foraging habitats in 1990 and 1991. All other analyses used χ^2 tests for association. Significance was accepted at $P < 0.05$. Sample sizes of various analyses differed due to missing data.

TABLE 1. Total number of foraging attempts by wintering Bald Eagles by foraging method and year along the Colorado River in Grand Canyon, Arizona, 1990–1991.

	Hunting live prey		Scavenging		Interspecific piracy		
Year	*n*	%	*n*	%	*n*	%	Total
1990	757	85.7	86	9.8	40	4.5	883
1991	380	88.4	15	3.5	35	8.1	430
Total	1137	86.6	101	7.7	75	5.7	1313

RESULTS

FORAGING METHODS, PREY USE, AND SUCCESS

Eagles foraged primarily by hunting live prey (Table 1). The relative proportion of hunting live prey increased from 1990 to 1991, scavenging decreased, and interspecific piracy increased (Table 1; $\chi^2 = 21.6$, df = 2, $P < 0.001$). Interspecific piracy was directed at Common Ravens (*Corvus corax*; $n = 55$, 98% successful) and Golden Eagles (*Aquila chrysaetos*, $n = 20$, 25% successful). Most foraging attempts were for rainbow trout or unknown fish assumed to be rainbow trout (n = 1,303, 99.2%); only 10 attempts (0.8%; 1 in 1990 and 9 in 1991, all unsuccessful) were for waterfowl.

Foraging success for both years combined was 72%; however, annual foraging success for all foraging methods combined declined from 76% in 1990 to 64% in 1991 ($\chi^2 = 20.3$, df = 1, $P <$ 0.001). Scavenging was the most successful foraging method (97%) and was more successful (χ^2 = 37.2, df = 2, $P < 0.001$) than piracy (79%) or hunting live prey (70%). The few unsuccessful scavenging attempts occurred when aerial attacks failed to secure dead trout from the river.

INFLUENCES ON FORAGING BEHAVIOR

Time of day. Hourly foraging patterns on days without human disturbance were different in 1990 compared to 1991 ($D = 0.15$, $P = 0.001$). Foraging attempts in 1990 exhibited morning and afternoon peaks ($D = 0.13$, $P < 0.001$), whereas foraging attempts in 1991 were distributed evenly throughout the day ($D = 0.06$, $P = 0.37$; Fig. 1).

Proximity to river shore. In the river, 97 (71%)

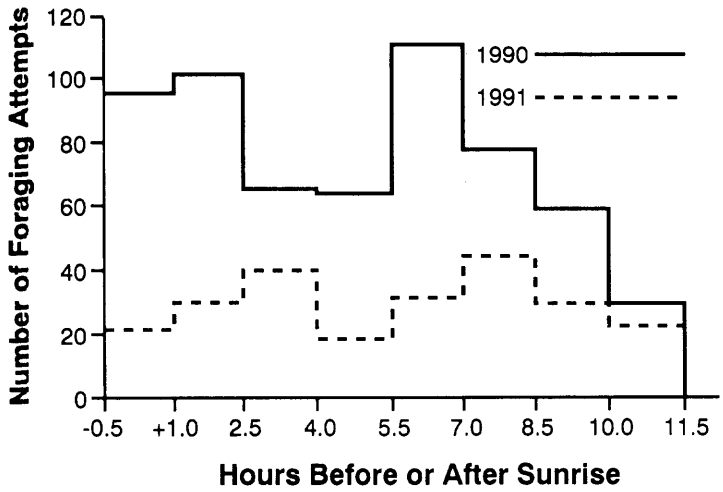

FIGURE 1. Hourly foraging attempts by Bald Eagles in the winters of 1990 and 1991 along the Colorado River in Grand Canyon, Arizona. Only foraging attempts during days without human disturbance were included (22 days in 1990, $n = 603$; 19 days in 1991, $n = 236$).

of 137 foraging attempts occurred <5 m from shore. Foraging success was greater within 5 m from shore (47%) than in deep water more than 5 m from shore (18%; $\chi^2 = 10.9$, df = 1, $P = 0.001$). More foraging attempts within 5 m from shore occurred in 1990 (95%) than in 1991 (51%; $\chi^2 = 31.5$, df = 1, $P < 0.001$).

Habitat. Foraging attempts were not distributed evenly among foraging habitats in either year (Table 2). Eagles foraged more in creek habitat in 1990 ($\chi^2 = 1358.7$, df = 3, $P < 0.001$) and 1991 ($\chi^2 = 304.5$, df = 3, $P < 0.001$) and less in river, pool, and shore habitats. Patterns of foraging attempts by habitat changed between years ($\chi^2 = 78.4$, df = 3, $P < 0.001$). Proportionally more foraging attempts occurred in creek habitat in 1990 compared to 1991, and more foraging attempts occurred in river and isolated pool habitat in 1991 compared to 1990. Overall foraging success for all prey types for both years combined was 75% in the creek, 41% in the river, 85% in isolated pools, and 100% on shore.

INFLUENCES ON FORAGING SUCCESS

Since 74% of the 1,331 total foraging attempts observed were for live trout in creek or river habitats, further analysis addressed the influences of age, foraging habitat, attack method, and prey abundance on success in those two habitats.

More foraging attempts were initiated by immatures (73%) than by adults (27%; Table 3), as a result of the predominance of immatures throughout most of the study period (Brown and Stevens, in press). Adults were more successful (74%) than immatures (66%) in capturing live prey from both habitats combined (Table 3). Adults were more likely to forage in creek (80%) than river habitats (20%), whereas immatures

TABLE 2. Number and percent of foraging events by age, habitat, and year for wintering Bald Eagles at and near the confluence of Nankoweap Creek and the Colorado River, Grand Canyon National Park, Arizona, 1990–1991. Percentages for the four habitats refer to the percent of total foraging events for that year only ($n = 886$ in 1990, 441 in 1991).

	Creek				River				Pool				Shore					
	1990		1991		1990		1991		1990		1991		1990		1991		Totals	
Age	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Adult	143	16	102	23	26	3	44	10	22	3	24	6	32	4	16	4	409	31
Immature	553	62	162	37	45	5	50	11	19	2	28	6	46	5	15	3	918	69
Totals	696	78	264	60	71	8	94	21	41	5	52	12	78	9	31	7	1327	100

TABLE 3. Log-linear model of associations between age, habitat, attack method, prey abundance, and success of Bald Eagle foraging attempts for live trout in Nankoweap Creek or the Colorado River, Grand Canyon National Park, Arizona, 1990–1991. Parameter estimates are listed only for effects resulting from the most parsimonious model.

Effect	Parameter estimate	χ^2	P
Age	0.375	214.8	0.000
Habitat	0.805	587.2	0.000
Method	0.058	85.0	0.000
Prey	0.134	145.1	0.000
Success	0.249	135.7	0.000
Age × habitat	0.169	7.4	0.006
Age × method	—	2.3	0.127
Age × prey	0.236	32.0	0.000
Age × success	−0.165	14.7	0.000
Habitat × method	0.335	38.4	0.000
Habitat × prey	0.182	12.9	0.000
Habitat × success	0.327	53.6	0.000
Method × prey	0.210	27.0	0.000
Method × success	—	0.2	0.629
Prey × success	0.052	10.8	0.001
Age × habitat × method	—	2.3	0.124
Age × habitat × prey	—	0.1	0.697
Age × habitat × success	—	2.9	0.086
Age × method × prey	—	0.2	0.652
Age × method × success	—	0.0	0.889
Age × prey × success	—	0.6	0.413
Habitat × method × prey	—	2.7	0.096
Habitat × method × success	−0.278	18.7	0.000
Habitat × prey × success	—	0.0	0.856
Method × prey × success	0.012	6.0	0.014
Age × habitat × method × prey	—	0.0	0.842
Age × habitat × method × success	—	3.0	0.080
Age × habitat × prey × success	—	0.0	0.855
Age × method × prey × success	—	0.0	0.862
Habitat × method × prey × success	0.141	7.3	0.006

foraged mainly in creek habitat (89%; 11% in river). Age was not significant in the log-linear model above a two-way association with habitat, success, or prey abundance, indicating the greater foraging success of adults was consistent by foraging habitat and prey abundance.

Overall, more foraging attempts occurred in creek (87%) than river habitat (13%), and creek foraging attempts were more successful (73%) than river attempts (38%; Table 3). Ground attacks (65%) were more common than aerial attacks (35%), but ground and aerial attacks were equally successful. However, proportions of ground to aerial attacks differed by habitat. In creek habitat, 69% of foraging attempts were ground attacks and 31% aerial attacks; in river habitat, 34% were ground attacks and 66% aerial attacks. In creek habitat, ground attacks were 71% successful and aerial attacks 78% successful; in river habitat, ground attacks were 62% successful and aerial attacks 25% successful.

Success rates were greater and more foraging attempts took place in creek habitat in a year of high prey abundance (Tables 3, 4). In 1990, 92% of foraging attempts occurred in creek habitat and 8% in river habitat; in 1991, 75% occurred in creek habitat and 25% in river habitat. The proportion of ground and aerial attacks also differed by prey abundance. In 1990, 72% of foraging attempts were ground attacks and 28% aerial attacks; in 1991, 49% were ground attacks and 51% aerial attacks. Success rates of ground and aerial attacks differed by prey abundance because, relative to aerial attacks, ground attacks were more successful when prey was more abundant (Tables 3, 4).

The four-way association between habitat, attack method, success, and prey abundance in-

TABLE 4. Percent foraging success on live trout in Nankoweap Creek or the Colorado River by wintering Bald Eagles by habitat, year, age, and attack method, Grand Canyon National Park, Arizona, 1990–1991.

Attack method by age	Creek				River				Both locations				Both years	
	1990		1991		1990		1991		1990		1991			
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Ground attack														
Adult	82	85	45	60	11	64	11	73	93	83	56	63	149	75
Immature	378	73	86	55	17	53	6	67	395	72	92	55	487	69
Totals	460	75	131	56	28	57	17	71	488	74	148	58	636	70
Aerial attack														
Adult	41	80	45	82	8	63	23	39	49	78	68	68	117	72
Immature	123	72	54	82	22	18	35	11	145	64	89	54	234	60
Totals	164	74	99	82	30	21	58	22	194	68	157	60	351	64
Grand totals	624	75	230	67	58	43	75	33	682	72	305	59	987	68

dicated a difference in success by habitat, attack method, and prey abundance (Table 3). Success of ground and aerial attacks in creek habitat was high and equal during high prey abundance, but success of ground attacks exceeded that of aerial attacks in river habitat (Table 4). In contrast, aerial attacks were more successful than ground attacks in creek habitat during prey scarcity while success of ground attacks in river habitat still exceeded that of aerial attacks in the river.

DISCUSSION

Foraging methods of Bald Eagles were dependent on prey abundance between years. Hunting for live prey was the predominant foraging method regardless of prey abundance, but the proportion of hunting live prey decreased when prey was more abundant. Scavenging was more frequent when carrion were plentiful, and interspecific piracy was more frequent during prey scarcity. Eagles along the Colorado River exhibited similar foraging methods to eagles along the Platte River in Nebraska (hunting 87%, scavenging 4%, and piracy 9%; Stalmaster and Plettner 1992), but hunted more live prey, scavenged, and pirated less compared to eagles at the Columbia River estuary, Oregon (57%, 24%, and 19%, respectively; Watson et al. 1991).

Prey scarcity caused a shift in geographic foraging patterns in the river. During prey scarcity, more foraging attempts occurred farther from shore where foraging success was lower. Since water depth was less than 3 m within 5 m of shore in the areas where foraging occurred (unpubl. data, Glen Canyon Environmental Studies, U.S. Bureau of Reclamation), eagles were more successful hunting for trout in shallow water. Foraging patterns of eagles in the Columbia River estuary were also dependent on shallow water less than 4 m deep, but no difference existed in success between deep and shallow water in the Columbia River estuary (Watson et al. 1991).

Foraging success also was dependent on prey abundance between years, with higher overall foraging success occurring in a year of high prey abundance. The success rate of hunting live prey was higher during high prey abundance, although success of scavenging and interspecific piracy was independent of prey abundance. Success of hunting and scavenging in my study area (70% and 97%, respectively) was similar to success on the Columbia River estuary (66% and 98%, respectively). However, success rates for piracy differed (79% and 46%, respectively; Watson et al. 1991). This difference was apparently due to the inclusion of intraspecific piracy in the Columbia River total, and the difference in target species. Most piracies in the Columbia River estuary were unsuccessfully directed against gulls (*Larus* spp.) which would drop prey into open water when eagles attempted piracy. In contrast, most piracies along the Colorado River were successfully directed at Common Ravens, which were unable to fly away with intact prey.

Changes in hourly foraging patterns also corresponded to changes in prey abundance. Eagles exhibited morning and afternoon peaks when prey was more abundant, whereas eagles foraged throughout the day during prey scarcity. I suggest that prey scarcity may have caused eagles to spend more time foraging each day.

Bald Eagles could choose to forage from four

habitats in close proximity, yet foraged mostly in creek habitat. This pattern was exhibited by all ages, attack methods, and levels of prey abundance. Foraging success was greater in creek than river habitat, so eagles presumably increased their food intake by foraging in creek habitat whenever possible.

Eagle foraging strategies were independent of age. Adults were more successful than immatures, similar to the success rates of adults and immatures reported from Glacier National Park, Montana (Shea 1978), and the Platte River, Nebraska (Stalmaster and Plettner 1992). This reflected a lack of experience in immatures, as younger eagles are less efficient at foraging than adults (Stalmaster and Gessaman 1984). Although immatures made proportionally more foraging attempts in creek habitat than adults, the higher success rate of adults was evident in all habitats. Higher adult success was independent of any combination of habitat, attack method, or prey abundance.

Bald Eagles were scarce along the Colorado River in Grand Canyon National Park prior to the construction of Glen Canyon Dam in 1963, and no concentration of wintering eagles was possible until the subsequent introduction and proliferation of rainbow trout (Brown et al. 1989). Dam operation altered the river so that it is no longer a naturally regulated aquatic ecosystem, the antithesis of national park resource goals. Although remnants of the native fish community persist in the new, artificial ecosystem, restoration of the native fish community to its original condition is virtually impossible due to introduced parasites and predators (Carothers and Brown 1991). The findings of my study suggest that maintaining or enhancing the river's exotic trout fishery for wintering Bald Eagles would benefit this endangered bird. Such action would also contradict current National Park Service policy, and could harm the remaining native fish. The challenge for future river and dam management is to reconcile these conflicts and set priorities appropriate for the new man-made ecosystem.

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