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FORAGING ECOLOGY OF NESTING BALD EAGLES IN ARIZONA

W. GRAINGER HUNT,[1] RONALD E. JACKMAN, AND DANIEL E. DRISCOLL
Predatory Bird Research Group, Long Marine Laboratory,
University of California, Santa Cruz, CA 95060 U.S.A.

EDWARD W. BIANCHI
Entrix, 7919 Folsom Blvd., Suite 100, Sacramento, CA 95826 U.S.A.

ABSTRACT.—We studied foraging ecology of nesting Bald Eagles (*Haliaeetus leucocephalus*) in Arizona during 1987–89, with emphasis on the influence of dams and river flow regulation. We examined diet, foraging modes, habitat selection, fish abundance, and factors associated with fish availability. Based on biomass, prey remains yielded 76% fish, 14% mammals, and 10% birds. On rivers, eagles primarily caught live fish as they spawned or foraged in shallow water, whereas, on reservoirs, most fish were obtained as carrion or as they floated moribund on the surface. Fish communities differed among river reaches and reservoirs, and ecological and life-history characteristics influenced vulnerability and seasonal differences in exploitation. Water temperature, a principal factor determining fish community structure among eagle territories, was also associated with temporal differences in fish availability, as was flow and turbidity. Few prey sources remained constant throughout the reproductive cycle, and prey and habitat diversity buffered temporal changes in prey availability. We conclude that dams benefit breeding eagles to the extent that they create water temperature discontinuities and additional aquatic habitats, some that support large populations of fish. However, environments modified by dams are not necessarily better for Bald Eagles than those on free-flowing sections of rivers; our data show that Bald Eagle reproduction in the two settings is nearly identical.

KEY WORDS: *Bald Eagle*; Haliaeetus leucocephalus; *dams*; *habitat selection*; *home range*; *piscivory*; *radiotelemetry*; *rivers*.

ECOLOGÍA DEL FORRAJEO DE ÁGUILAS CALVAS NIDIFICANDO EN ARIZONA

RESUMEN.—Estudiamos la ecología de forrajeo de águilas calvas (*Haliaeetus leucocephalus*) nidificando en Arizona durante 1987–89, con énfasis en la influencia de los embalses y la regulación del flujo de los ríos. Examinamos la dieta, modos de forrajeo, selección de hábitat, abundancia de peces, y factores asociados con la disponibilidad de peces. Tomando como base la biomasa, los restos de presas arrojaron 76% peces, 14% mamíferos, y 10% aves. En los ríos, las águilas ante todo capturaron peces vivos cuando estos desovaban o forrajeaban en aguas someras, mientras que, en los reservorios, la mayoría del pescado fue obtenido como carroña o cuando flotaban moribundos sobre la superficie. Las comunidades de peces difirieron entre los limites de los ríos y las características ecológicas y de su historia de vida las cuales influyeron en la vulnerabilidad y las diferencias estaciónales en la explotación. La temperatura del agua, un factor primordial determinante de la estructura de la comunidad íctica entre los territorios de las águilas, fue asociada además con las diferencias temporales en disponibilidad de peces, tal como lo fue con el flujo y la turbidez. Pocos recursos de presas permanecieron constantes a través de todo el ciclo reproductivo, y las presas y diversidad de hábitats amortiguaron los cambios temporales en la disponibilidad de presas. Concluimos que los embalses benefician las águilas que están reproduciéndose en el sentido en que crean discontinuidades en la temperatura y hábitats acuáticos adicionales, algunos

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[1] Present address: The Peregrine Fund, 5568 West Flying Hawk Lane, Boise, ID 83709 U.S.A.; e-mail address: regniarg@aol.com

de los cuales soportan grandes poblaciones de peces. Sin embargo, los ambientes modificados por las represas no son necesariamente mejores para las águilas pescadoras que aquellos que están en secciones de libre flujo en los ríos; nuestros datos muestran que la reproducción de las águilas pescadores en los dos escenarios son cercanamente idénticos.

[Traducción de César Márquez]

Population persistence in raptors and other territorial birds depends on an aggregate of breeding locations that contribute to above-replacement-rate reproduction (Hunt and Law 2000). Conserving high-quality sites requires knowledge of key components, some being physiographic, others depending on the ecology, behavior, and life-history characteristics of associated biota. Of particular interest are factors relating to food acquisition. Reproductive success requires that breeding pairs have *sustained* access to prey within efficient commuting distance (Royama 1970). For species with prolonged breeding cycles (ca. 5 mo for North American eagles), during which numerous phenological events transpire, food continuity may involve switching from one prey type to another over the course of the nesting season (Jamieson et al. 1982, Edwards 1988).

Prey remains collected from nests of inland-breeding Bald Eagles (*Haliaeetus leucocephalus*) often show dietary diversity. This has been observed not only for populations as a whole, but for individual nests (Todd et al. 1982, Jackman et al. 1999). Thus, it is tempting to hypothesize that prey variety and, by inference, environmental variation within the foraging range are important components of Bald Eagle territories in some regions (Grubb 1995).

From January 1987–June 1989, we investigated the effects of dams and flow regulation on the nesting population of Bald Eagles in central Arizona (Driscoll et al. 1999). We obtained information on the spatial and temporal aspects of foraging. We recorded shifts of eagle prey use, foraging behavior, and ranging patterns that followed temporal variation in factors influencing prey availability. We found that water temperature and clarity, the structure of various riverine and lacustrine habitats, and life-histories and behavior of prey species were interrelated with respect to food availability.

STUDY AREA

General Description. Our study centered on Bald Eagle breeding territories along the Salt and Verde rivers in central Arizona (Fig. 1), a generally open, desert landscape of the Upper and Lower Sonoran Life-Zones (Lowe 1964, Brown 1998). Eagles nested at elevations ranging from 329–1719 masl. Riparian environments in these regions are composed of Sonoran Riparian Deciduous Forest and Woodlands Biome, Sonoran Riparian Scrubland Biome, and the Sonoran Interior Strands Biome. Uplands in the Lower Sonoran Life Zone are all within Sonoran Desertscrub Biome (Brown 1998). Upper Sonoran Life Zone (Brown 1998) vegetative composition near Bald Eagle breeding territories includes Great Basin Conifer Woodland, Interior Chaparral, and Semidesert Grassland Biomes. Mean annual precipitation ranges from 39 cm at higher elevations to 25 cm in the low desert where temperatures may reach 50°C.

The central Arizona landscape has been greatly altered by human activity. Cattle grazing, particularly after railway development in the late 1800s, resulted in dramatic erosion (Hastings 1959, Hastings and Turner 1965, Hayden 1965). This and woodcutting reduced riparian forests to a scattering of isolated groves and trees. Soil loss drained near-surface aquifers, creating drier soil conditions, and rivers became muddy torrents following rains. With the increased need for flood control, water storage, and irrigation, five impoundments were constructed on the Salt River and two on the Verde River during the early 1900s. Riverine environments downstream of the reservoirs were changed by flow regulation and sediment filtration, and upstream by migrations of fish populations such as common carp (*Cyprinus carpio*) and catfish (Ictaluridae) out of the reservoirs.

Fisheries. Three native species of fish, appropriate for eagle exploitation, remain in substantial numbers within the study area: desert sucker (*Catostomus insignis*), Sonora sucker (*C. clarki*), and roundtail chub (*Gila robusta*) (Minckley 1973). Introduced species of potential importance to eagles in rivers and/or reservoirs include channel catfish (*Ictalurus punctatus*), bullhead (*Ameiurus nebulosus* and *A. natalis*), flathead catfish (*Pylodictis olivaris*), common carp, black crappie (*Pomoxis nigromaculatus*), yellow bass (*Morone mississippiensis*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*M. dolomieui*), bluegill (*Lepomis macrochirus*), green sunfish (*L. cyanellus*), and walleye (*Stizostedion vitreum*).

Fish distribution in central Arizona, as elsewhere, is strongly influenced by water temperature (Vannote et al 1980, this study). Trout (Salmonidae) inhabit cool headwaters. Suckers, smallmouth bass, and then channel catfish increase in abundance as water warms downstream With increasing water temperature, carp and catfish become the primary species in size categories suitable for Bald Eagle foraging. When a river enters a reservoir, perciforms (bass, perch, and crappie) predominate, although carp and catfish contribute importantly to overall fish biomass in the reservoir. Water temperature and volume released from the reservoir influence the fish community below the dam. Cool releases from the hypolimnion of deep, stratified reservoirs favor sucker populations. If the reservoir is shallow or unstable and

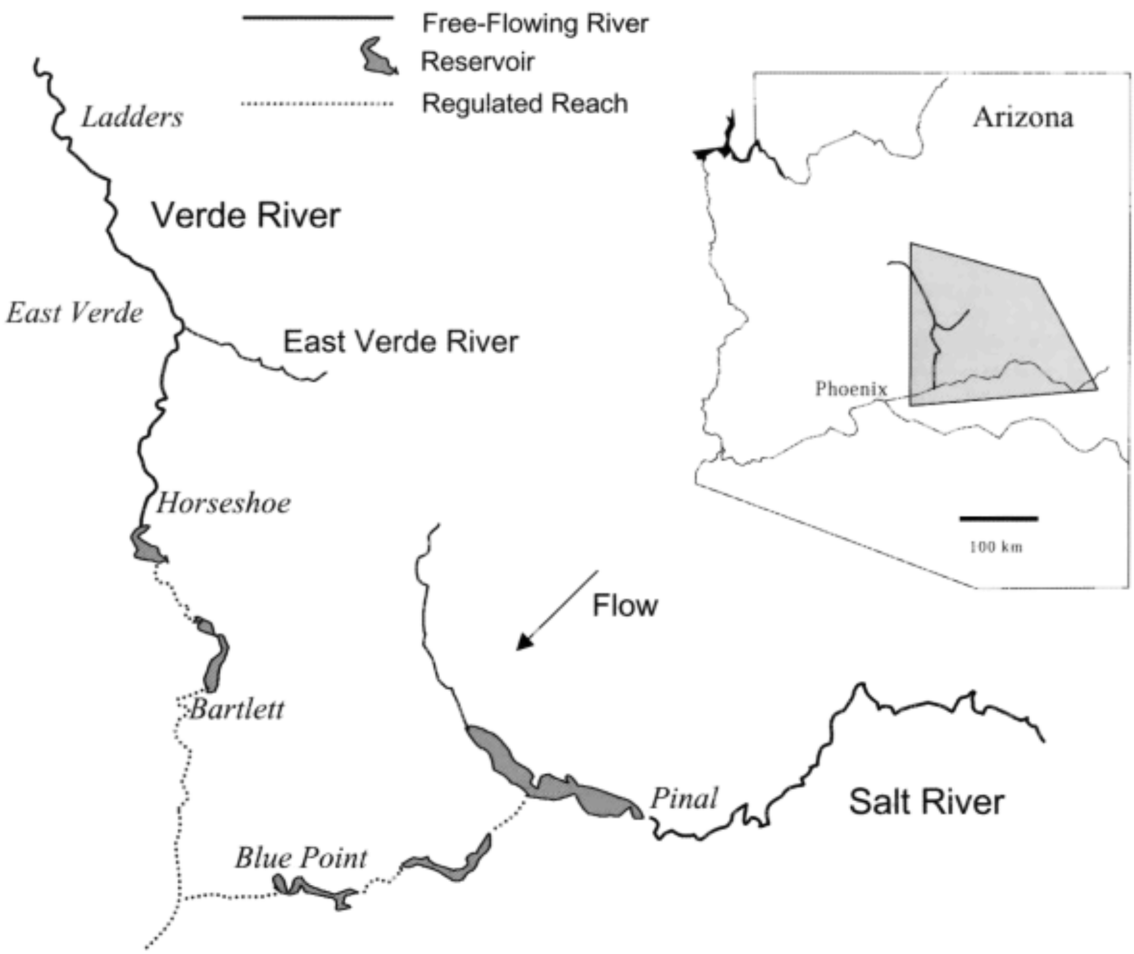

Figure 1. The Salt and Verde river systems of central Arizona. The six names in italics identify breeding territories where Bald Eagle foraging was studied with radio telemetry.

fails to maintain a cool hypolimnion, or if releases issue from the epilimnion, warm releases favor carp and catfish in the river reach below the dam. During spring, spawning runs of carp and catfish from downstream reservoirs may augment riverine fish populations.

Study Sites. We studied Bald Eagle foraging at six breeding territories (defined here to include the foraging range) chosen to compare regulated with unregulated (i.e., free-flowing) environments (Fig. 1). All six territories have been occupied by eagles since the 1970s (Driscoll et al. 1999). Two breeding territories (Ladders and East Verde) were on free-flowing rivers far from reservoirs. Two other pairs (Bartlett and Blue Point) occupied settings in which all flows were regulated by dam releases, i.e., reservoirs releasing cold water and fed by other dams upstream. The remaining two breeding territories (Horseshoe and Pinal) included both reservoir systems and the free-flowing rivers that fed them.

METHODS

Telemetry. We used radio-controlled bow nets, power snares, and noosed fish (Jackman et al. 1993, 1994) to capture territorial eagles for radio-tagging. We attached 65-g transmitters with a backpack configuration of teflon ribbons adjoined with cotton string over the carina to permit eventual loss of the radio (Hunt et al. 1992, McClelland et al. 1994). Mercury (activity) switches changed the pulse rate when tilted from near-vertical to horizontal (Kenward 2001). We refined signal interpretation on the basis of frequent visual verification.

From the early brooding period to fledging, tracking teams collected data in 8-d sessions separated by 6-d periods of no data collection. The objective was to obtain uninterrupted, minute-by-minute records (time lines) of movements and activities of radio-tagged eagles. To overcome the bias associated with observer location, trackers spread out to strategic viewing sites and maintained communication by hand-held radios. Tracking teams of three to five members later conferred to eliminate duplicate data points. To reference eagle locations, habitat variables, and prey, we marked river centerlines and reservoir shorelines depicted on USGS topographic maps to show 1-km and 0.1-km intervals. If we could not identify the eagle's location to the level of even a 1-km segment, we marked the location within larger zones positioned between familiar landmarks.

We measured variables at prey-strike points as soon as possible after a foraging event but without disturbing the eagle. Recorded information included attack method and aquatic habitat type, as follows: "pools" are depressions in the streambed, with hydrologic control in the downstream end and low current velocities relative to prevailing streamflow; "runs" are moderately deep, usually narrow channels with relatively fast current, but little or no white water; "riffles" are characterized by shallow, fast-moving water flowing down gradients and over substrates usually no larger than small boulders; "pocket water" usually contains larger boulders, with fast water interspersed across the width of the stream among frequent pockets of quiet water; "cascades" are steep gradient white water with less than 10% quiet water (Hunt et al. 1992). Microhabitat features measured at strike points included water depth, water temperature, and turbidity (Secchi disk). We collected evidence (e.g., scales) of prey species identity, and estimated prey size and whether it was obtained alive or as carrion.

Prey Delivery. Observers recorded prey deliveries to the nests from points permitting clear views of nest bowls and at distances of 125–400 m, typically beginning when young were 2–3 wk of age. Prey items were assigned to general taxonomic categories (e.g., class), then to more specific categories (e.g., family, species), where possible. For fish, diagnostic features included fin and scale characteristics, body and mouth shapes, jaw configurations, barbel presence, caudal peduncle thickness, and markings. Observers noted their confidence in each identification; items identified with low confidence were assigned to a higher taxonomic level. We sometimes confirmed identification with body parts (e.g., scales) collected at eagle foraging sites. We did not distinguish between desert and Sonora suckers. We estimated prey size by comparing the item with the length of the eagle's bill or with objects of known size in the nest.

Analysis of Tracking Data. Time line tracking data consisted of 22 742 records of the movements and activities of nine radio-tagged adults in six breeding territories, for a mean of 2527 records per tagged eagle. We recorded the number of minutes an eagle remained at a location and the frequency of visits to each location. The first measure (time) offered a relatively poor estimate of area use compared to relocation frequency. Consider an example in which an eagle loafed for 146 min at a location 300 m downstream of the nest (in sight of the nest), then flew 2 km upstream where it perched for 5 min at each of three locations, some 200 m apart. At the last of these, the eagle caught a fish, after which it returned to the nest area where it spent 62 min. Clearly, a time-based assessment awards small significance to the foraging area where the eagle spent only 2% of its time. By contrast, the relocation-based appraisal recognized each of the 0.1-km segments (or larger zones) where the eagle perched. Weighting each location equally as a measure of use was supported by our data: in 80% of observed foraging events, the eagle perched within sight of the foraging location just before the event, and in 70% of cases, the eagle appeared to have seen the prey before leaving the perch.

Each perching visit to a 0.1-km segment received a score of one point. If the eagle left a location and entered another 0.1-km segment along the river, but then returned to the original location, the latter received another point. Segments visited repeatedly thereby received the most points. The large number of nest visits overshadowed other relocation scores; however, eliminating the nest area from the analysis was inappropriate because the nest vicinity was often an important foraging area. Therefore, we used the prey delivery data to estimate the percentage of foraging events occurring in the nest vicinity. This became the relocation percentage for the nest area, and percentages for all other areas within the home range were adjusted accordingly so the total was 100%.

Collection and Analysis of Prey Remains. *Collection.* We collected prey remains within and below nests at five of the six breeding territories studied (one nest was on an inaccessible pinnacle) and at 16 other breeding sites in Arizona. Collections occurred during the middle to late part of the brood-rearing period and again after the young had fledged. We attributed variation in the amount of remains present to removal by the adults (observed) and to the activities of woodrats (*Neotoma* spp.) and other scavengers. We collected ca. 2 L of fine nest lining from each nest for scale analysis to detect soft-boned fish (e.g., trout, chub) (Jackman et al. 1999).

Analysis. We collected 5–10 individuals of differing sizes of each fish species expected to occur in the eagles' diet. We weighed and measured each fish, then parboiled it to remove all flesh. We weighed, dried, and labeled all bones for reference.

We developed regression equations to relate bone length to total body length for each species (Hunt et al. 1992, Jackman et al. 1999). Because unattached bones were often from the same fish, we used the following procedure to avoid duplication: first, we determined the 95% confidence intervals from each equation to determine the probable range of total length represented by the bones. For a given collection and species, we calculated fish total length from each bone and then sorted all like bones. Bones with the most entries and relatively low confidence intervals were examined first. We grouped pairs of these bones of the same size (<1.0 mm difference or <5 mm for broken bones), e.g., left and right opercula. We marked each pair and the remaining odd entries as individual prey items. We next matched the opercula(s) from one fish with other bones whose confidence intervals for total body lengths overlapped with those computed from the opercula. Because different parts of the same fish had specific proportional relationships (e.g., ±2.0 mm for sucker opercula and clavicles), we eliminated those entries that were eclipsed by the confidence intervals, a procedure that left the fewest numbers of unmatched parts and, thus, the fewest possible number of individual fish represented. Results underestimated total fish numbers to the extent that matched parts may have been from different fish.

We calculated total mass for the selected (nonduplicate) fish prey items, using length-to-mass equations from this study and from Carlander (1969, 1977) and Becker (1983). We subtracted the mass of bones and scales (from regression equations) plus 5% of total mass (estimated unavailable biomass) to calculate the edible biomass for each prey item. We identified nonfish remains from museum reference collections and then used standard body mass for each species less 10% for inedible parts.

Fish Sampling. Objectives of fish sampling within eagle territories were to identify: (1) relative abundance of prey fish, (2) seasonal changes in their distribution, with emphasis on availability to eagles (e.g., fish moving into shallow water), (3) spawning and its effect on fish availability, and (4) effects of water management on prey fish availability.

Fish abundance, activity, and distribution. We conducted both roving and fixed-point visual surveys. In roving surveys, one or two biologists (depending upon flow) walked along the river bank, noting abundance and activity of fish, aquatic habitat, depth, location (within standard 0.1-km segment), and water temperature. We also observed fish activity and behavior from fixed points. Prior to surveying, we compiled information on fish communities in the various river reaches, tributaries, and reservoirs, including Arizona Game and Fish Department (AGFD) and U.S. Fish and Wildlife Service reports and field data from D. Henrickson (AGFD), M. Jakle (U.S. Bureau of Reclamation), and C. Zeibell (Arizona Cooperative Fisheries Unit).

To verify our observational data and to determine gonadal development, we sampled fish in representative habitats with gill nets and throw nets, and occasionally by snorkeling surveys. We removed all collected fish from the system, many of which were used in the prey reference series. We conducted an electrofishing survey at the East Verde territory just after the eagle nesting season.

Aquatic habitat surveys. We surveyed aquatic habitat distribution in four of the six eagle territories. We mapped sections of rivers and tributaries within eagle home ranges into basic habitat units, including pools, runs, riffles, pocket water, and cascades, as defined by Hunt et al. (1992). We differentiated between two types of riffles: channel-riffles, which become runs during moderate flow increase, and bar-riffles which remain as riffles under a variety of flows. Bar-riffles are characterized by the presence of a gravel/cobble bar oriented diagonally or perpendicularly to flow. As flow increases, water depth and velocity increase only partially in bar-riffles, whereas the amount of shallow water increases overall due to spreading of water across the gravel/cobble bar. We mapped reservoirs according to distributions of shallow water areas. We obtained river flow and reservoir water surface elevation data from agencies maintaining gaging stations.

Carrion and Waterbird Surveys. We conducted periodic surveys on rivers and reservoirs to assess temporal availability of carrion. We sampled representative stretches of reservoir shoreline where we expected carrion to accumulate, e.g., coves, bends, and especially where rivers entered reservoirs. We slowly followed shorelines by boat, identifying and measuring all carrion fish, birds, and mammals encountered. We noted factors contributing to death, e.g., trauma, evidence of spawning, fishing paraphernalia. On rivers, we selected one to three 100-m areas in each territory where carrion was likely to accumulate, and with particular attention to channel bends. We surveyed for waterbirds from one or two points offering wide views per territory, or by making counts while traveling along water bodies (e.g., during carrion surveys), noting the species and numbers present.

RESULTS

Diet. We identified 19 species of fish, 26 birds, 16 mammals, and three reptiles from (1) the remains of 2601 prey individuals collected from nests, under perches, and after foraging events at 23 breeding territories, and (2) observations of 713 prey items delivered to nests (Table 1). Mean biomass percentages for each class in remains from all sites were 75.5% fish, 14.3% mammals, and 10.2% birds. Four groups accounted for nearly all fish biomass: catfish (mainly channel catfish), sucker (desert and Sonora suckers), carp, and perciforms (mainly largemouth bass, black crappie, and yellow bass). Seven taxa exceeded 15% of fish biomass at one or more of 23 territories sampled in central Arizona: sucker at 12 territories, carp at 12, channel catfish at 10, largemouth bass at six, flathead catfish at three, crappie at two, and yellow bass at two.

Comparisons of prey remains with prey deliveries over similar time frames consistently showed that biomass estimates from remains overrepresented mammals and birds over fish, and catfish over suckers and perciforms (Hunt et al. 1992). In three territories where items and deliveries were within comparable time frames, 7 of 56 fish (10.3%) identified in remains were suckers, whereas 124 of 342 (33.2%) fish deliveries were suckers (χ^2 = 13.1, df = 1, P = 0.0003). Remains versus delivery ratios for catfish in these samples were 24:56 (42.8%) and 56:342 (16.4%) (χ^2 = 47.6, df = 1, $P < 0.0001$). An experiment involving a blind sample of 45 fish fed to a captive eagle supported our field data in that soft-boned fishes tended to be underrepresented, e.g., 100% of carp appeared in the remains, 80% of catfish, 60% of the somewhat softer-boned suckers, and only 8% of trout (T. Gatz and M. Jakle, unpubl. data).

As expected, suckers were the most common prey for pairs nesting on cool, free-flowing reaches nearest the headwaters or at sites offering access to regulated river reaches downstream of hypolim-

Table 1. Prey biomass estimates from prey remains and observed prey deliveries (in italics) for 11 Bald Eagle territories on the Salt and Verde rivers where sample sizes exceeded 40 items. Letters in parentheses refer to dam releases from the cool hypolimnion (C) or the warm epilimnion (W).

Breeding Area	Setting	*N*	Percent Biomass						
			Suckers	Carp	Catfish	Perciforms	Mammals	Birds	Other
Ladders	Free-flowing river	79	8	48	20	1	18	5	0
deliveries		*130*	*45*	*33*	*17*	*0*	*3*	*0*	*2*
East Verde		95	5	47	27	2	12	5	2
deliveries		*103*	*14*	*49*	*17*	*8*	*6*	*0*	*6*
Redmond		156	5	18	55	1	12	4	5
Pinal	Free-flowing river and reservoir	107	5	19	47	13	8	8	0
deliveries		*46*	*0*	*10*	*55*	*27*	*0*	*3*	*5*
Horseshoe		95	1	8	36	31	4	19	1
deliveries		*48*	*0*	*34*	*11*	*40*	*2*	*0*	*13*
Blue Point	Regulated river (C) and reservoir	85	10	7	21	22	18	22	0
deliveries		*152*	*28*	*2*	*9*	*41*	*8*	*8*	*4*
Bartlett		47	55	11	18	7	9	0	0
deliveries		*234*	*66*	*2*	*9*	*15*	*6*	*0*	*2*
Orme	Regulated river	56	45	4	3	2	34	12	0
Ft. McDowell		62	66	5	5	1	18	5	0
Cliff	Regulated river (W) and reservoir	45	0	46	18	27	5	4	0
"76"	Creek	59	5	38	2	1	41	13	0

netic dam releases (Table 1). Perciforms were taken mainly in the reservoirs. Eagles obtained carp primarily in warm, free-flowing reaches upstream of reservoirs and in a river fed by epilimnetic releases (Table 1). Catfish (channel and flathead) were widely utilized, the highest numbers taken from free-flowing river reaches and in a reservoir (Alamo) with only seasonal inflow (Haywood and Ohmart 1986).

Estimates of mammal biomass from remains exceeded 25% at six breeding territories. Most frequently identified were black-tailed jackrabbit (*Lepus californicus*) and cottontail rabbit (*Sylvilagus audubonii*). We recorded only 32 mammals among 713 prey items observed delivered to nests (4.5% of items) despite a more substantial representation in prey remains from those nests (18.3%). We attribute this disparity to the greater use of mammals early in the breeding season and to biases associated with bone persistence.

Waterbirds were more important to Bald Eagles in early winter than during the nesting season, particularly at territories containing reservoirs. In winter, the percentages of birds observed taken (as compared with fish) were 50% in December, 56% in January, and 13% in February, as compared with 5% in March, 1% in April, and 0% in May. The most commonly recorded birds taken among 30 identified were American Coots (*Fulica americana*, $N = 15$) and Eared Grebes (*Podiceps nigricollis*, $N = 8$).

Conditions of Prey Acquisition. Eagles took some fish species only in riverine conditions, others only from reservoirs, and some from both. Of the seven important fish taxa recorded during prey delivery observation, numerical ratios of their origin in rivers versus reservoirs at four territories containing both environments were as follows (river : reservoir): yellow bass (0:31), crappie spp. (0:40), largemouth bass (2:22), flathead catfish (3:5), channel catfish (4:17), sucker spp. (105:0), and carp (3:30). In reservoirs, eagles obtained most fish as carrion (or moribund), i.e., 66% of 125 fish of known status (excluding piracies) were obtained from reservoirs as carrion, whereas 12% of 201 fish from rivers were carrion.

Suckers. At least 83% ($N = 114$) of suckers were alive when taken, 5% were pirated, 3% were carrion, and 9% were of unknown status. Bald Eagles caught them mainly in riffles while they spawned or foraged. Of 64 depth measurements at strike points for live suckers, 80% were in water ≤30 cm in depth; mean depth at strike points of these 51 shallow water captures was 16.4 cm (SD ± 7.3).

Carp. Eagles obtained carp from both rivers and reservoirs. In rivers, eagles caught them in the shallows of runs and riffles, 17 of 20 strikes in water less than 36 cm deep. We were unable to determine under what conditions carp were captured in reservoirs.

Catfish. We estimate from prey collections that channel catfish contributed almost three times the biomass as flathead catfish (301 182 g versus 92 304 g, respectively). Excluding piracies, we observed nesting Bald Eagles taking channel catfish on 51 occasions: 75% on reservoirs and 25% on rivers. On reservoirs, 81% of 26 catfish of known status were obtained as carrion, whereas on rivers, 27% of 11 were carrion. Although the sample of conditions at strike points for live channel catfish in rivers was small, it differed from those noted for other species. Eagles captured five in pocket water, three in runs, and none from riffles. The mean of six depth measurements was 58 cm (SD ± 28.1). We occasionally observed catfish swimming near the surface in riverine pools (Van Daele and Van Daele 1982), and "blooms" of carrion channel catfish (ca. 20 cm long) appeared in late spring at two reservoirs (Horseshoe and Roosevelt).

Perciforms. At four breeding territories containing reservoirs (Bartlett, Saguaro, Horseshoe, and Roosevelt), we recorded delivery of 61 largemouth bass, 51 black crappie, 41 yellow bass, and 14 others (mainly sunfish). Eagles obtained these perciforms mainly as carrion from the reservoir or as they lay moribund at the surface. Of 76 dead or moribund perciforms found in carrion surveys on these same reservoirs, 29 were yellow bass, 15 largemouth bass, 13 black crappie, eight bluegills, four smallmouth bass, four green sunfish, and three walleye. The yellow bass and black crappie were apparent victims of spawning stress, whereas many of the largemouth fatalities were angler-related.

Birds and Mammals. Coots were attacked when they foraged in the grassy shallows of reservoirs. Eagles caught grebes and waterfowl either by stooping repeatedly at groups in open water or by approaching low (<1 m) over the surface, snatching the prey in passing. We observed no attempts at live mammals.

Habitat Use. We observed eagles foraging in riffles disproportionate to their occurrence along the river. At Ladders, 54% of 58 prey captures were in riffles, the latter composing only 5% of riverine habitat within the 22-km foraging range of the eagles. At East Verde, 46% of 61 observed foraging events were in riffles, compared to 15% availability within 19 river km. Along 2.3 kilometers of river at Bartlett, 73% of 119 observed foraging attempts were in riffles compared with 8% availability. At Blue Point, 32% of 28 attempts were in riffles compared with 4% availability. The frequency of riffle use in part reflected the high proportion of sucker captures in those territories. As noted, eagles captured suckers mainly in riffles, carp most often in runs, and channel catfish in pocket water and runs.

In 162 measurements of turbidity at strike points for live fish, 136 (84%) were in water that was "clear to the bottom." When rivers became turbid during prolonged periods of snowmelt, eagles tended to forage elsewhere, such as in clear tributaries.

At the four breeding areas containing both riverine and reservoir environments, eagles mostly foraged from reservoirs (>50% of locations). At two territories where eagles nested on the river 3.6 km and 7.0 km from reservoirs, 51% and 61% of total relocations were on the reservoirs, respectively. For a radio-tagged pair whose nest was situated where a river entered a reservoir, 85% and 86% of relocations were on the reservoir. At a territory where the nest was about 2 km from both river and reservoir, 59% of relocations were on the reservoir. Among a biomass total of 113.5 kg of delivered prey items recorded at these four territories, 28.4%, 65.9%, 93.9%, and 48.4% were obtained from the reservoir. Of 641 forage attempts recorded at these territories, 386 (60%) were on reservoirs.

Foraging Range. *Free-flowing river.* We compared eagle foraging ranges at two territories (Ladders and East Verde) situated on the free-flowing Verde River far upstream of the dams and reservoirs (Fig. 1). The nests of both pairs were on cliffs overlooking the river: the two nests at Ladders were directly over bar-riffles, but the East Verde nest was about 1 km from the nearest bar-riffle. At both territories, the null hypothesis of random selection by the eagles of 1-km segments containing bar-riffles was rejected (Chi-square tests, $P < 0.005$). At East Verde, 72% of mainstem relocation points were within seven 1-km segments, in the aggregate containing 100% of the bar-riffles within the 19 km

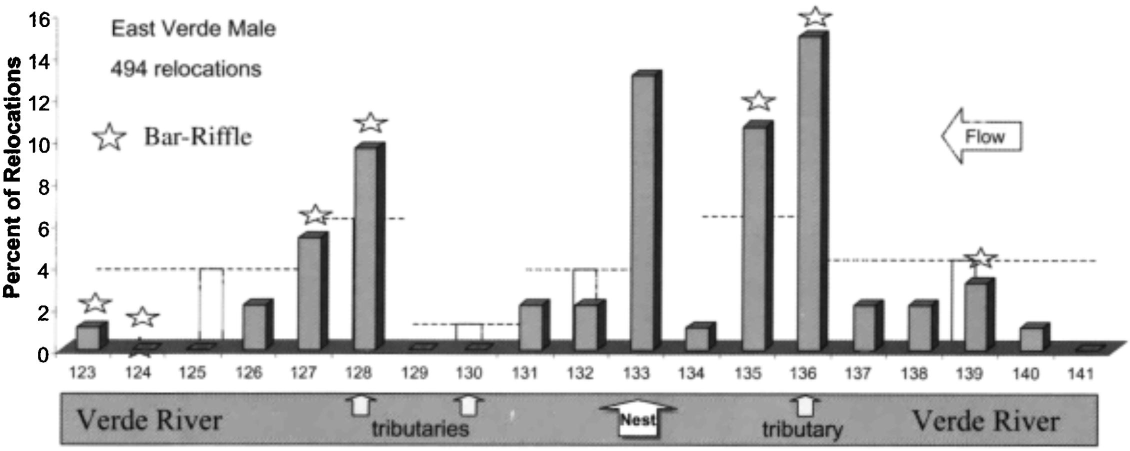

Figure 2. Foraging range of the radio-tagged breeding male Bald Eagle at the East Verde territory. Relocation percentages in the nest vicinity were adjusted according to the proportion of observed prey deliveries from those 1-km segments (see Methods). Open bars quantify cases in which trackers could not precisely locate the eagles; dotted lines extending laterally from open bars indicate zones of eagle occupancy for the imprecise locations (tributary relocation percentages not shown).

foraging range (123–141 km), but containing only 21% of the available channel-riffle habitat (Fig. 2). At Ladders, 54% of visits within the 22 km range were within the six 1-km segments containing bar-riffles.

There were clear, seasonal shifts in prey and habitat use (Fig. 3). For example, in March, when the Verde River was turbid, 17 of 18 prey items recorded at the East Verde territory were mammals. In April, the East Verde male traveled up two relatively clear tributaries to forage on spawning suckers. By early May, he was foraging almost exclusively in the mainstem Verde River, taking carp and catfish. His use of river sections downstream of the nest peaked during the mid-point of the brood cycle, then shifted dramatically to the area upstream of the nest containing a large bar-riffle.

Regulated river and reservoir. The home ranges of the Bartlett and Blue Point pairs (29 and 26 river-km, respectively) both contained a deep-release (cool) regulated river section below a reservoir fed by a regulated reach. At both breeding territories,

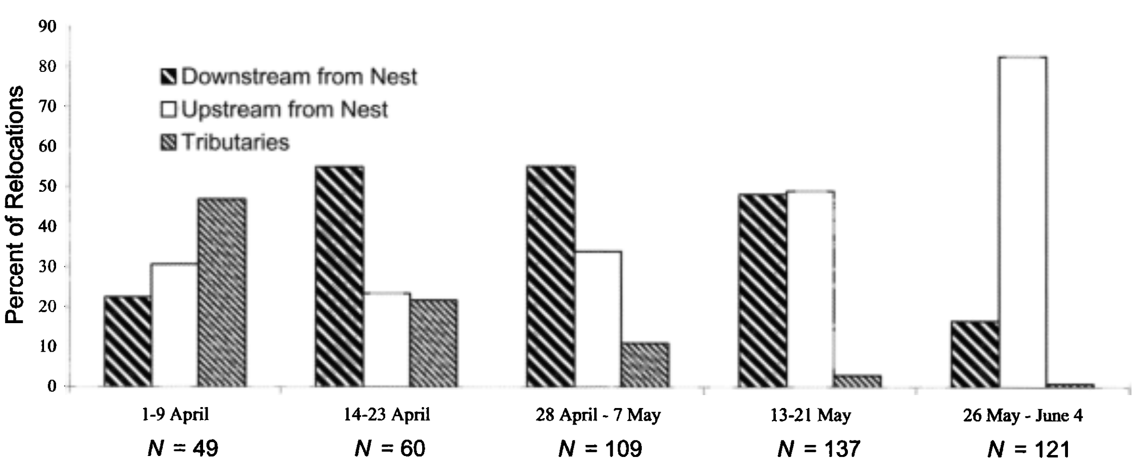

Figure 3. Chronological shifts in ranging by the radio-tagged male at the East Verde territory to areas outside the nest vicinity.

most river visits by radio-tagged eagles were in the vicinity of the first large cliff downstream of the respective dams. Suckers were abundant in riverine environments at both territories. At Bartlett, a large bar-riffle was present near the nest cliff. This 1-km segment and the only two others containing bar-riffles received the three highest relocation scores (51%, 8%, and 8% of 164 river relocations of the male) within a home range containing 13 km of river. At Blue Point, the 1-km segment with the highest river relocation score (56% of 314 river relocations of the male in two breeding seasons) contained a large cliff above a bar-riffle. At both territories, the eagles traveled downstream as far as 9 km to forage on suckers in early spring, but as the zones of suitable sucker spawning temperatures moved upstream, the birds responded accordingly. At Bartlett, this phenomenon is apparent when one divides the 1989 nesting season (26 February–20 May) into three equal periods. In the early period, 35% of relocations by the breeding male were to the area within about 2 km of the nest (3.6 km downstream of the dam), but these rose to 59% and 86% in the middle and late periods. Relocations to the area 3–10 km downstream of the nest declined from 65% to 36% to 14% during the three periods. In 20 comparisons of river temperatures between the nest vicinity and a location about 5 km downstream, the downstream temperatures were invariably higher (paired t-test, $t = 11.3$, $P < 0.0001$). During the early period when the eagle traveled downstream so frequently, the mean stream temperature was 13.5°C at the nest vicinity and 15.5°C at the downstream location. Importantly, Sonora suckers spawn at 14–18°C. Sucker spawning peaked in the downstream reach in mid-March and ceased by mid-April, when spawning in the upstream section reached its peak.

Both the Bartlett and Blue Point eagles frequently perched and foraged in reservoir environments: 51% of 334 relocation points by the Bartlett male were on the reservoir, and 59% ($N = 765$) for Blue Point. Waterbirds (mainly American Coots and Eared Grebes) attracted eagles at both territories to the reservoir in winter. In spring, the main inducement for reservoir use in both areas was the presence of carrion (or moribund) fish, mainly yellow bass (Saguaro), black crappie (Bartlett), and largemouth bass (both reservoirs).

Free-flowing river and reservoir. The Horseshoe and Pinal breeding territories both contained a free-flowing river section that entered a reservoir. The Horseshoe nest was at the upstream end of a reservoir, and the Pinal nest was 7 airline km upstream of a reservoir. All four radio-tagged adults foraged primarily at the reservoir inflow. Even though the Horseshoe nest was at the inflow, the use of the river was relatively low (male = 15%, female = 18%). Resources offered by these reservoirs included wintering waterbirds and carrion fish. As in the other four territories, the radio-tagged birds at Horseshoe and Pinal changed their patterns of home range use during the course of the nesting season. In winter, the Horseshoe and Pinal adults traveled downstream to the body of the reservoir where waterbirds were concentrated. By March they began foraging closer to the nest, and both pairs traveled further to forage during the late stages of the nesting season. Home range sizes for the Horseshoe and Pinal pairs were 17 and 27 river-km, respectively.

Environmental Setting and Nesting Success. We compared reproductive performance for the period 1980–90 among breeding territories (productive at least once during that period) in modified versus unmodified environments. Productivity (mean young fledged ±SE/nest year) of pairs in areas altered by dam construction (1.07 ± 0.11, $N = 12$ territories, 89 nest-years) was almost identical to that of pairs in areas not altered by dams (1.04 ± 0.10, $N = 9$ territories, 71 nest-years) ($t = 0.08$, $P = 0.94$).

DISCUSSION

Bald Eagle pairs foraged on a wide variety of prey, the distribution within each diet was rarely skewed toward a single taxon. If anything, we underestimated the degree of dietary diversity by lumping some taxonomic groups, by underrepresenting the pre-egg-laying diet when birds and mammals made important contributions to fat storage, and by not including the 4–9-wk post-fledging period when dependent young remained in their natal territories. Our results were consistent with those of Grubb (1995) who hypothesized that mammals may help to fill a dietary gap during periods of high turbidity (e.g., snowmelt) when fish are less visible.

Underlying the diverse and variable diet of nesting eagles were the ordering of gross habitat features within the landscape (e.g., reservoirs, rivers, tributaries), the variety of aquatic habitats within them (e.g., riffles, runs, pools, reservoir inflows), the changing factors that influenced the timing of prey availability (e.g., flow, temperature, and turbidity), and the diverse natural history of each prey species (e.g., spawning cycles, foraging behavior). Our radio-tracking data and observations of prey deliveries at the intensively studied territories suggested that prey sources for nesting eagles rarely remained constant throughout the reproductive cycle.

Our findings support that prey and habitat diversity are important to many Bald Eagle pairs in Arizona, allowing for continuous food availability through a lengthy breeding season. Thus, it would seem that dams may benefit Bald Eagles to the extent of creating water temperature discontinuities and additional aquatic habitats, some with large populations of fish. However, environments modified by dams were not necessarily better for Bald Eagles than those on free-flowing river reaches, given that reproduction in the two settings was nearly identical. Eagles do appear to benefit from the presence of exotic fish which form major components of the eagles' diet in both regulated and unregulated environments.

Even so, current conditions are not necessarily more supportive of Bald Eagles than were those in the pristine (pre-livestock) landscape when more robust, infiltrated soils likely slowed the transport of water to rivers which thereby maintained more consistent flows over the yearly cycle of rainfall (Olmstead 1919, Hastings 1959, Hastings and Turner 1965, Hayden 1965). Moreover, some stream courses, now seasonally dry, were perennial in past centuries and doubtless supported fish populations. Since the 1980s, at least nine pairs of Bald Eagles have fledged young on free-flowing reaches and tributaries that are probably now more turbid than they would have been before the grazing era.

Today, Bald Eagles nesting upstream of reservoirs feed primarily on four fish species: Sonora suckers, desert suckers, carp, and channel catfish. Of these, only the suckers are native to Arizona. However, five other species of fish of appropriate size categories were once present: Colorado pikeminnow (*Ptychocheilus lucius*), razorback sucker (*Xyrauchen texanus*), flannelmouth sucker (*Catostomus latipinnis*), roundtail chub (still fairly common), and bonytail chub (*Gila elegans*) (Minckley 1973). Several reports attest to the early abundance of native fishes (Rostlund 1952, Minckley and Alger 1968, Haase 1972). Native Americans used them extensively for food, as did the settlers that came to the region in the mid-1800s (Davis 1982). Even as late as the early 1900s, fish were so common in the lower Salt and Gila rivers that they were sold as feed for domestic animals and as fertilizer (Minckley 1973). Now, the Colorado pikeminnow, the razorback sucker, and the bonytail chub are federally listed as endangered.

Although we cannot be certain if the communities of native fishes occurring in the pristine rivers supported nesting eagles, it is quite possible that the four species of suckers, augmented by waterfowl and spawning runs of pikeminnow and possibly others, formed a complete prey base. Because suckers feed and spawn in shallow water, they are ideal prey for eagles. Our study suggests that eagles would have benefited if the native fishes were to have spawned at different times. Such would be expected, considering that any coevolved community of fishes would tend toward spawning differentials in time and space (some ascending tributaries) because of niche similarity and competition among fry.

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