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FORAGING ECOLOGY OF BALD EAGLES ON A REGULATED RIVER

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ABSTRACT.—We studied the habitat, foraging behavior, and prey of eight pairs of Bald Eagles (*Haliaeetus leucocephalus*) nesting along northern California's Pit River where flows and reservoir elevations were regulated by five hydroelectric facilities. Prey remains (N = 1166) and photographic data (N = 117) indicated that eagles fed on a variety of fishes (88%), birds (9%), and mammals (4%), but one species, Sacramento Sucker (*Catostomus occidentalis*) dominated the diets of all pairs. Bald Eagle prey utilization at Britton Reservoir was directly related to the abundance of fish species inventoried by surface gill nets. Bald Eagles ate Sacramento Sucker and Tule Perch (*Hysterocarpus traski*) as carrion in late May, June, and July when these species became numerous on the surface of the reservoir. Eagles nesting near relatively small run-of-river reservoirs downstream of Britton Reservoir foraged in both lacustrine and riverine habitats. On the river sections, eagles selected hunting perches near pools rather than runs or riffles. In pools, live suckers were taken mainly in shallow areas where there was no surface turbulence. Inventories indicated that fish were less common in pools than in runs or riffles, suggesting that physical conditions promoting prey vulnerability were more important to eagles than those influencing prey density. However, eagles did not use a large section of river where suckers of appropriate sizes for eagles were uncommon.

Hábitos de alimentación de Águila Cabeciblanca en un río de corriente regulada

EXTRACTO.—Hemos estudiado el hábitat, la conducta en la alimentación, y las presas de ocho parejas de Aguila Cabeciblanca (*Haliaeetus leucocephalus*) que anidaban a lo largo de río Pit en California del norte. En este río el volumen del flujo del agua y la cantidad de ella en las represas estaban regulados por medio de cinco plantas hidroeléctricas. Los residuos de presas (N = 1166) así como datos fotográficos (N = 117) indicaron que las águilas se alimentaron de una variedad de peces (88%), de aves (9%), y de mamíferos (4%); pero una especie de pez perteneciente a la especie *Catostomus occidentalis* dominó la dieta de todas las parejas. La utilización de las presas de Águila Cabeciblanca en la represa Britton, estuvo directamente relacionada con la abundancia de especies de peces cogidos por redes tendidas en la superficie del agua. Hacia fines de mayo, en junio y julio, las águilas comieron carroña de peces *C. occidentalis* y *Hysterocarpus traski,* cuando estas especies se hacen numerosas en la superficie del estanque. Águilas que anidaban cerca de relativamente pequeños estanques, los que se llenan con agua de la represa Britton, se alimentaron tanto en hábitats lacustres como fluviales. En las secciones rivereñas, las águilas seleccionaron las perchas de observación para cazar prefiriendo la cercanía a albercas que a corrientes rápidas o turbulentas. En las albercas, peces vivos fueron cogidos principalmente en áreas de poca profundidad donde no había turbulencia superficial. Los conteos indicaron que los peces fueron menos numerosos en albercas que en secciones de rápidos y turbulencias; lo que sugiere que las condiciones físicas que promueven la vulnerabilidad de las posibles presas, fueron más importantes para las águilas que las condiciones que influencian la abundancia de las presas. Sin embargo, las águilas no usaron una gran sección del río donde los peces del tamaño apropiado para ellas no fueron comunes.

[Traducción de Eudoxio Paredes-Ruiz]

Foraging success of raptors depends on the composition, densities, life histories, and behaviors of prey species, and the physical and biotic elements of habitat that contribute to prey vulnerability. Raptor foraging patterns may coincide with prey abundance (Hunt et al. 1992a) or depend on the distribution

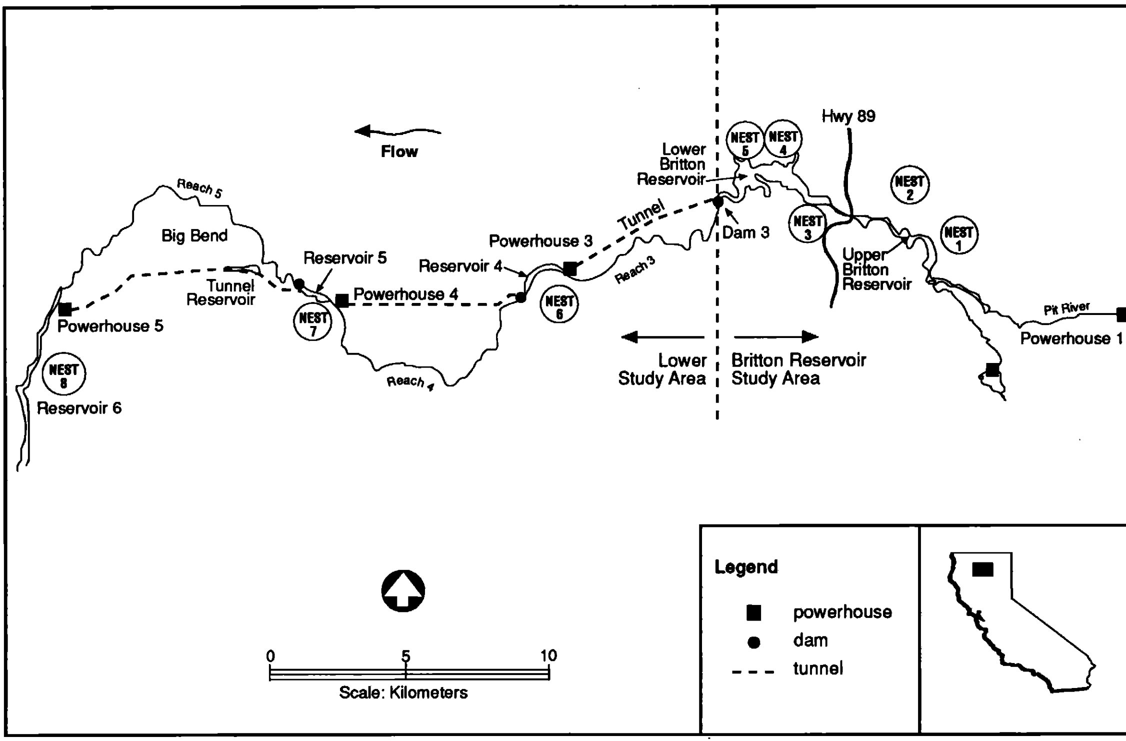

Figure 1. The Pit River study area in northern California.

of specific habitats where prey are vulnerable but not necessarily abundant (Hunt and Ward 1988). Life history, behavioral, and ecological factors affecting vulnerability may differ among prey species and habitats.

In this paper, we present the results of a two-year study on the foraging ecology of Bald Eagles (*Haliaeetus leucocephalus*) on northern California's Pit River, where flows are controlled by five hydroelectric facilities occurring along 70 river km (study area). Eight Bald Eagle nesting territories are known in the area, and in winter and spring eagle numbers are augmented by migrants.

To explore the interrelationships between eagle diet, foraging habitat selection, and factors affecting prey availability, we investigated: 1) the distribution of nesting and wintering eagles in the study area using visual surveys and telemetry, 2) diets of the eagles, 3) habitat use in both lacustrine and riverine habitats, 4) river habitat distribution, 5) distribution, relative abundance, and size classes of prey species, and 6) how each major prey fish species became vulnerable to Bald Eagles.

STUDY AREA

The Pit River originates in the Warner Mountains of northeastern California and flows through several broad, irrigated valleys to Fall River Mills where it enters a narrow, steep-sided canyon that extends for 90 km to Shasta Reservoir. Our study area included 70.3 km of this canyon, from the river section upstream from Britton Reservoir downstream to Reservoir 6 (Fig. 1). Within this zone are 24.5 km of reservoirs (Britton Reservoir and Reservoirs 4, 5, and 6) and 45.8 km of flowing, regulated river (Reaches 3, 4, and 5). Rather than producing electric power at Dams 3, 4, and 5, water is transported from them in underground conduits to powerhouses (turbines) located 10–16 river km downstream near the inflow of the next reservoir.

Because of habitat differences, we distinguish between Britton Reservoir (13 km long, 520 ha) and the mainly riverine environment downstream from it (Lower Study Area) where two relatively small run-of-river (currented) reservoirs (Reservoirs 4 and 5, 42 ha and 13 ha respectively) lie between river sections 9.6 to 15.9 km in length. In discussions of the river reaches, we sometimes differentiate between the upper (upstream) and lower (downstream) halves of each reach.

The area around Britton Reservoir is primarily Ponderosa Pine (*Pinus ponderosa*) forest (elevation ca. 860 m MSL); Sierran mixed-conifer forest is the dominant habitat type in the lower study area (elevation at Pit 6 Dam ca. 430 m MSL). Rainfall averages about 1 m/yr. Recreational use peaks during May–October and includes fishing and camping throughout the study area, and boating on Britton Reservoir.

In warmer months, the level of Britton Reservoir fluctuates with power demand, resulting in a highly variable pattern of drawdown (1–2 m/wk) during weekdays and refilling during weekends. Flashboards raise the height of the dam almost 2 m and increase generating capacity; they are removed in winter when increased flows result in spillage over the dam. The reservoir is often turbid with algae, particularly in the warmer months.

The three river reaches (3, 4, and 5) are confined to narrow canyons and have coarse-textured substrates, mostly cobbles and boulders covered with algae. During spring runoff, flow rates in the reaches are about 100 m^3/sec and, rarely, up to 565 m^3/sec. In the summer, Dams 4 and 5 provide minimum flow releases into the river sections of 1.4–4.2 m^3/sec on behalf of fisheries (D. Bowers pers. comm.). During our study, no water was released from the dam at Lake Britton (Dam 3), but about 1.4 m^3/sec seeped from the dam and underground springs. Because none of the warm turbid water from Britton Reservoir was released into Reach 3 in summer, water was cooler and clearer than in reaches 4 and 5. The fish community in Reach 3 reflected these differences.

METHODS

Bald Eagle Distribution and Habitat Selection. We determined the distribution of Bald Eagles in the study area by censuses conducted from helicopters, boats, and vehicles. We made 82 helicopter censuses from a Bell Jet Ranger helicopter, flying at 95–125 km/hr downriver or along reservoir shores above the tree tops. Weather permitting, these censuses were done weekly from March 1983 to December 1984, usually in the early morning. On Britton Reservoir, we censused Bald Eagles and waterfowl on 36 surveys (approximately 2/mo) from a boat moving slowly along the shore. At Reservoir 4, we censused Bald Eagles and waterfowl 104 times from a vehicle slowly moving along a road adjacent to the reservoir.

We recorded the age class of each eagle observed. For this analysis, juvenile/immature birds (dark head), subadults (mottled head), and near-adults ("dirty" white head) were all grouped as subadults; only birds with completely white heads were considered adults. For each eagle observed, we noted its location, distance to water, perch type, and habitat. We also collected information on waterfowl distribution, noting the location, number and species of waterfowl observed. Location data were based on a 0.1 km scale following the river centerline.

We affixed radio transmitters to seven nesting adults (5 females, 2 males) and nine subadults of unknown natal origin. The radio-tagged adults included four nesting females at Britton Reservoir (nests 1, 3, 4, and 5). In the lower study area, we radiotagged the adult male at Nest 7 and both members of the pair at Nest 6. We mounted nine of the transmitters on retrices (Young 1983); the other seven were backpack-mounted, using teflon ribbons secured with cotton string over the carina. We captured eagles with either floating, noosed fish (Frenzel and Anthony 1982, Cain and Hodges 1989) or with padded leghold traps (Harmata 1985).

We used telemetry to locate and identify individual eagles during surveys. Telemetry monitoring sessions of radio-tagged adults were conducted by ground vehicle or boat throughout the morning hours in both breeding and non-breeding months. For analysis of relocation data within the study area, we considered only the first detection per day per location and excluded instances of soaring flight; we defined a relocation as a movement of at least 100 m. Outside the study area, we recorded the movements of radio tagged eagles on periodic aerial telemetry surveys around the northern California region.

From a boat and from the shoreline we observed eagles foraging in the reservoirs. A dirt road paralleling the river allowed access during tracking, although the forest canopy often obscured our view. We therefore constructed eight blinds along the forested river banks to allow observations of foraging in riverine habitat. We chose blind locations based on concurrent telemetry data and occupied several of them each morning. When a foraging attempt was observed, and after the eagle departed, we measured: 1) water depth, 2) substrate characteristics (e.g., cobble, sand, sediment), 3) surface turbulence (visually estimated), 4) water velocity (time for a floating object to travel 1 m), 5) stream habitat type (e.g., pool, run, riffle, see below), and 6) vegetation at the strike point. Even if the exact strike point could not be observed, certain data could be obtained if conditions such as depth and surface turbulence were homogeneous over wide areas. If possible, we visually identified the prey at the time it was taken, and also searched the foraging site later for prey remains.

Bald Eagle Diets. We determined diet by: 1) collecting prey items in and below nests and under perches, 2) observing foraging eagles, and 3) time-lapse photography. We identified prey remains by comparison with a reference collection of study area fishes, using scale keys (Casteel 1972, 1973), and by comparison with museum bird and mammal collections. Using bone length to fish length and fish length to weight equations empirically derived from fish captured during electrofishing (see below), we computed estimated total weights for non-duplicate prey items. By subtracting bone and scale weights (plus 5% total weight to account for inedible biomass) from fish weights in the prey reference collection, we obtained values of edible biomass. To calculate size and minimum number of fish in scale samples we determined scale age (Bagenal and Tesch 1978). We used standard weights for estimating non-fish prey biomass (Steenhof 1983, Dunning 1984).

We placed time-lapse movie cameras (Minolta Super-8 with intervolometers and light-activated switches) at three nests in 1983. These cameras, installed in boxes 3–5 m above nests, exposed one frame per 90 seconds during daylight.

Habitat Mapping. River habitat downstream from Britton Reservoir was mapped in 1984. The distribution of riverine habitats did not change with the flow releases under study (2.8–8.5 m^3/sec), but might change with spring run-off flows (>50 m^3/sec). Aerial photos and ground checking were used to classify river sections into the following categories: "Pools" are depressions in the streambed, with a major hydraulic control at the downstream end. Throughout most of the length and width of the pool habitat, current velocities are low relative to prevailing

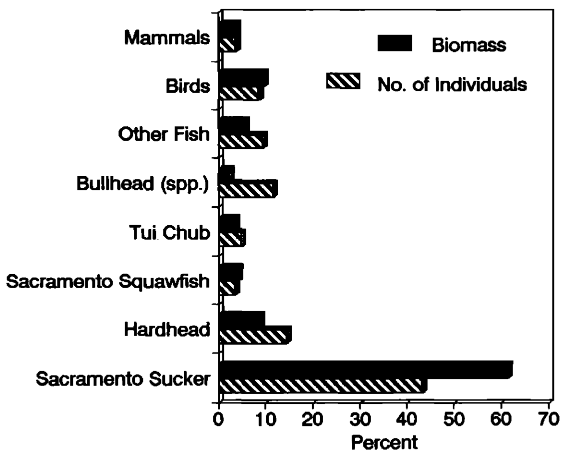

Figure 2. Diet of Bald Eagles in the Pit River study area as determined from a sample of 1166 prey items identified in remains (representing an estimated 938.1 kg of edible biomass).

streamflow. "Runs" are relatively deep, usually narrow channels. There is little or no white water in this habitat type and the hydraulic control is less distinct than in a pool; current velocity is relatively fast. "Riffles" are characterized by relatively shallow, fast-moving water flowing down gradients less steep than cascades and over substrates usually no larger than small boulders. "Cascades" are steep gradient white water with less than 10% quiet water. "Pocket water" usually contains boulders, with fast water liberally interspersed across the width of the stream. Pockets of quiet water (1–3 m in diameter) are frequent.

The principal river pools where eagles foraged were mapped on aerial photos and ground-checked in summer 1984. A digital planimeter was used to determine the area of various pool characteristics under normal summer flows and three experimental release flows. Assessment at each flow level included: 1) the presence and surface area of three water depth categories (less than 0.6 m (classified as "shallow"), 0.7–1.2 m, and over 1.3 m), 2) the presence or absence of surface turbulence (a rippling of the water surface that obscures visibility into the pool), 3) the estimated percentage of green algae or macrophyte coverage, 4) the total pool area, and 5) the length of the pool tail (the shallow area at the downstream end of the pool).

Prey Fish Distribution and Abundance in Reservoirs. Data on fish abundance and distribution in reservoirs were collected by gill netting, electroshocking, and carrion surveys. Vondracek et al. (1989) detailed the gill netting and electrofishing procedures. To summarize, gill nets were set monthly at either of two coves on Britton Reservoir using variable mesh gill nets set at surface (0–4 m), midwater (4–8 m), and bottom locations (8–16 m). We selected coves known to be eagle foraging areas. Nets were 36–38 m long and 1.5–1.8 m deep. Five nets at each depth were set for a minimum of 4 hr during all sampling periods. Variable mesh in equal-sized panels (3 m) ranged from 20–152 mm. The electrofishing surveys were conducted monthly at 27 stations on Britton Reservoir, although activities were suspended during the second Bald Eagle breeding season (March–July 1984) to avoid biasing Bald Eagle food habit data (electrofishing can kill fish and create a carrion food source for eagles). A Cofelt boat-mounted electrofisher was generally set at 350 volts DC and 60 pulses per second (Vondracek et al. 1989). Electrofishing stations were about 50 m in length and concentrated in shoreline locations. A diversity of shoreline habitats were electrofished, including shallow and deep water with various bottom substrates. Each captured fish was measured and weighed (to develop a length-weight regression relationship) and then released.

We surveyed carrion semi-monthly by boat 34 times on Britton Reservoir and 32 times on the three reservoirs in the lower study area. We used hoopnets to sample dead and injured fish emerging from powerhouse turbines at the inflow tailrace of Reservoir 4.

We compared the biomass and frequency of fish species in eagle prey remains at Britton Reservoir to the biomass and relative abundance of fish species in electrofishing samples and in surface (0–4 m) gill nets. We excluded fish from the comparison if they were less than the minimum size found as prey (250 mm for most species).

Prey Fish Distribution and Abundance in the River. Snorkeling surveys conducted in early summer and fall were used to determine fish abundance and distribution in the stream sections (see Baltz et al. 1987 for methods). Surveys were stratified by reach, river segment, and habitat, and were selected to cover various habitats within each stream section. Two to four snorkelers worked in an upstream direction starting below a selected habitat (see Baltz et al. 1987). Survey lengths were determined by habitat length and ranged from 25–150 m; 5–20 minutes were required to complete each survey. Seventy-three stream locations were surveyed four times each; data from 31 surveys were eliminated from the analysis because of poor visibility. Sampling area sizes were calculated from measurements of river lengths and widths. Each fish estimated to be over 50 mm SL (standard length: snout to base of tail) was recorded.

We obtained information on fish behavior from blinds above two pools in Reach 4 (July, August, and October of 1984) and from incidental observations. At half-hour intervals from 0600–1130 H, we identified, counted, estimated the size, and noted the location and activity of all fish visible in the pool. When visibility was low, we estimated overall fish activity by noting the number of rises during the observation period.

RESULTS

Eagle Occurrence in the Study Area. During the study period, paired eagles occupied eight nesting territories: five at Britton Reservoir and one each at reservoirs 4, 5, and 6 (Fig. 1). All nest sites were within 1 km of reservoirs. Only one was within 100 m of shore, and this nest was in the area least disturbed by humans. All nests but one were in mature Ponderosa Pines; Nest 8 was in a Douglas-fir (*Pseudotsuga menziesii*).

During our study, mated adults remained near their nesting territories throughout the year. They generally laid eggs in late February and early March with young fledging in mid- to late June. The eight pairs fledged 17 young in 15 nesting attempts during the two years of study. Fledglings departed from the study area in late July or early August. We radiotracked five individuals on northward migrations apparently directed toward salmon runs in Canada or Alaska (Hunt et al. 1992b).

We observed the greatest number of eagles during January and February (13.5 birds per helicopter survey); subadults represented 37% of the total. During this time, subadult eagles were attracted to the powerhouse tailrace at Reservoir 4 where small fish from Britton Reservoir passed through the turbines and became available as carrion. Fewer eagles were observed along reservoirs and river sections in March and April when adults were incubating or perched near nests. In May, June, and July, 33% of all eagles were subadults. However, by early August, virtually all subadults had vacated the study area; they comprised only 5% of total sightings in September and October and 2% in November and December. All seven of the subadults radiotagged in winter later frequented the Klamath Basin 120 km to the north, and three subsequently returned to the study area.

Diet. Bald Eagles in the Pit River study area fed on a variety of prey species taken either alive or as carrion. Fish comprised 87%, birds 9%, and mammals 4% of the 1166 items in our samples (Fig. 2). Sacramento Sucker (*Catostomus occidentalis*) was the most important fish species (numbers of individuals and biomass) taken by eagles in all parts of the study area, followed by Hardhead (*Mylopharodon conocephalus*) and Sacramento Squawfish (*Ptychocheilus grandis*) (Table 1). Lower Britton Reservoir eagles utilized less suckers and more cyprinids—namely Hardhead, Tui Chub (*Gila bicolor*), and Sacramento Squawfish—than in the other regions.

Chi-square comparisons of prey remains data with those collected by time-lapse cameras at individual nests and in total (Table 2) did not suggest that larger species were over-represented in remains because of larger and more persistent bones (see Todd et al. 1982). The results also did not indicate that Tui Chub, a relatively delicate species, was under-represented. Sample sizes for the time-lapse data were larger than for prey remains; some remains were likely dropped or taken from the nest by the eagles while other prey items may have been entirely consumed.

Of 17 species of birds identified in prey remains collected throughout the study area, all but 2 were waterbirds (Table 1). Birds were most numerous in prey samples collected in winter and spring and were absent in those obtained in July through October. Waterbird numbers in the study area were highest in winter and lowest in summer, but the number of species was highest (20) in spring. Canada Geese (*Branta canadensis*) were the most abundant (786 of 2608 bird records) and were present throughout the year. American Coots were the second most common (N = 576) but were observed only during fall and winter. Other common waterbirds were gull (*Larus* spp., N = 196), Common Merganser (*Mergus merganser*, N = 155), Double-crested Cormorant (*Phalacrocorax auritus*, N = 147), American Widgeon (*Anas americana*, N = 100), and Mallard (*Anas platyrhynchos*, N = 99). There was no significant association between numbers of the five most common waterbird species found in Bald Eagle prey remains and relative abundance of these five species recorded in waterbird surveys throughout the study area (Spearman rho = 0.20, $P > 0.05$).

Foraging on Britton Reservoir. The five pairs of bald eagles nesting on Britton Reservoir foraged in all portions of the reservoir, but rarely visited the river sections upstream or downstream. The linear ranges along the reservoir of three radio-tagged adult females were 0.7, 2.4, and 2.7 km. Although we radiotagged no breeding male eagles on Britton Reservoir, visual observations suggested that their foraging ranges were similar to those of the radiotagged females.

The eagles foraged on carrion and moribund fish, as well as live prey. We observed 42 forage attempts (52% successful) including 22 (52%) in open water or flowing reservoir habitat, 17 (41%) in cove, backwater, shallow gravel bar, or marsh habitat; 3 (7%) were piracies from Osprey (*Pandion haliaetus*) and Great Blue Heron (*Ardea herodias*). Prey taken were fish (N = 22), namely Sacramento Sucker, Carp (*Cyprinus carpio*), Hardhead, and small fish, probably Tule Perch (*Hysterocarpus traski*). At least 8 fish (36%) were taken as carrion.

Eagles flying out from shore over deep water took carrion fish or attacked fish swimming at or near the surface. Alternatively, eagles foraged in reservoir shallows, particularly in coves where they launched their attacks at live fish from perches. Fish spawned in and around the mouths of tributaries in coves where the clear inflow of springs and creeks in-

Table 1. Number and edible biomass of fishes, birds and mammals found in Bald Eagle prey remains in five subunits of the Pit River study area. Remains were collected in and below nests and from below perches, during all seasons.

	BRITTON RESERVOIR				LOWER STUDY AREA					
	UPPER NESTS 1, 2		LOWER NESTS 3, 4, 5		RESERVOIR 4 NEST 6		RESERVOIR 5 NEST 7		RESERVOIR 6 NEST 8	
	NO. (%)	% BIO-MASS	NO. (%)	% BIO-MASS	NO. (%)	% BIO-MASS	NO. (%)	% BIO-MASS	NO. (%)	% BIO-MASS
Fish										
Sacramento Sucker	284 (52.3)	72.8	84 (24.9)	44.9	80 (51.0)	60.2	32 (38.1)	32.2	24 (54.6)	68.5
Bullhead sp.	84 (15.5)	3.1	39 (11.5)	2.0	4 (2.5)	2.0	6 (7.1)	0.2	3 (6.8)	0.4
Hardhead	63 (11.6)	7.2	66 (19.5)	14.3	24 (15.3)	7.6	9 (10.7)	6.2	6 (13.6)	8.8
Tui Chub	21 (3.9)	2.6	30 (8.9)	8.2	5 (3.2)	2.9	0 (0.0)	0.0	0 (0.0)	0.0
Sacramento Squawfish	19 (3.5)	3.6	17 (5.0)	6.6	6 (3.8)	5.9	1 (1.2)	0.7	1 (2.3)	1.6
Other[a]	25 (4.6)	3.3	61 (18.1)	11.6	17 (10.8)	6.2	6 (7.2)	4.5	1 (2.3)	0.4
Total (% of total)	496 (91.4)	92.6	297 (87.9)	87.6	136 (86.6)	84.8	54 (64.3)	43.8	35 (79.6)	79.7
Birds[b] (% of total)	30 (5.5)	4.9	29 (8.6)	8.5	14 (8.9)	11.2	26 (30.9)	46.3	3 (6.8)	7.2
Mammals[c] (% of total)	17 (3.1)	2.5	12 (3.5)	3.9	7 (4.5)	4.0	4 (4.8)	9.9	6 (13.6)	13.1

[a] Other fish species (and total number of occurrences) included: 8 Channel Catfish (*Ictalurus punctatus*), 8 Carp, 38 minnows (Cyprinidae sp.), 24 crappie (*Pomoxis* sp.), 14 Tule Perch, 3 Rainbow Trout, 7 trout (*Salmo* sp.), 6 Largemouth Bass, and 2 sunfish (Centrarchidae sp.)

[b] Birds included: 29 American Coot (*Fulica americana*), 18 Dabbling ducks (*Anas* spp.), 11 Mallard, 10 geese (Anserinae), 8 grebes (Podicipedidae), 6 Tundra Swan, 5 Common Merganser (*Mergus merganser*), 4 unidentified birds, 3 Ruddy Duck (*Oxyura jamaicensis*), 2 Great Blue Heron, 2 gull (*Larus* sp.), 1 Double-crested Cormorant, 1 Common Goldeneye (*Bucephala aclangula*), 1 Ring-necked Pheasant (*Phasianus colchicus*), and 1 Screech Owl (*Otis kennicottii*).

[c] Mammals included: 12 Muskrat (*Ondatra zibethica*), 8 California Ground Squirrel (*Citellus beecheyi*), 7 Western Gray Squirrel (*Sciurus griseus*), 5 rabbits (Leporidae), 5 unidentified squirrels (Sciuridae), 3 Black-tailed Deer (*Odocoileus hemionus*), 2 Mountain Beaver (*Aplodontia rufa*), 2 Domestic Cow (*Bovus domesticus*), 1 Yellow-bellied Marmot (*Marmota flaviventris*), and 1 Striped Skunk (*Mephitis mephitis*).

creased fish visibility to eagles in the otherwise turbid reservoir.

We occasionally observed bottom feeders such as sucker and catfish swimming slowly near the surface of Britton Reservoir. Surface gill netting and hydroacoustic surveys indicated that frequency and diversity of fish swimming near the surface were greatest at dusk, intermediate at dawn, and lowest at midday, and that fish were most abundant near the surface during the warmer months (Vondracek et al. 1989). During the nesting season, Bald Eagle foraging occurred mostly in the morning. Of 236 prey deliveries recorded by time-lapse cameras at three nests (Nests 5, 6, and 8) totaling 98 camera-days, 49.6% occurred between 0600–1100 H, 29.2% between 1100–1600 H, and 21.2% occurred between 1600–2100 H.

Fish carrion was available on Britton Reservoir in late spring and early summer. In June and July, we found 12.9 items per survey (range = 3–30) compared with 1.7 items per survey from August through May (range = 1–6). Sacramento Sucker and Tule Perch represented 57% and 35%, respectively, of 99 carrion fish found in the June–July surveys. Many of these fish had apparently died from spawning stress, and some of the Tule Perch counted in the surveys were still alive, floating moribund at the surface on their sides. Some Sacramento Squawfish and Hardhead were killed by anglers. We were unable to determine whether significant numbers of dead fish were stranded during reservoir level fluctuations, but we occasionally found dead suckers along flat, grassy shorelines of Britton Reservoir and other backwaters in the study area.

Fish Abundance Versus Eagle Diet at Britton Reservoir. Sacramento Sucker comprised only 11% of the number of fish in electrofishing samples on Britton Reservoir, but because of their large size

Table 2. Number and biomass of fish species identified in the Pit River study area by time-lapse photography and prey remains collected over the same periods, Nest 5 from 23 May to 3 July, Nest 6 from 29 May to 30 June, and Nest 8 from 11 June to 5 July.

	NEST 5[a]				NEST 6[b]				NEST 8[c]			
	REMAINS		TIME-LAPSE		REMAINS		TIME-LAPSE		REMAINS		TIME-LAPSE	
SPECIES	NO.	BIOMASS (g)	NO.	BIOMASS (g)	NO.	BIOMASS (g)	NO.	BIOMASS (g)	NO.	BIOMASS (g)	NO.	BIOMASS (g)
Sac. Sucker	6 (23.1%)	6406 (43.1%)	14 (26.4%)	7049 (32.1%)	11 (52.4%)	9010 (72.1%)	24 (82.9%)	15 995 (88.7%)	15 (88.2%)	9558 (92.8%)	28 (80.0%)	12 731 (84.3%)
Hardhead	11 (42.3%)	5258 (35.4%)	11 (20.8%)	4685 (21.3%)	2 (9.5%)	838 (6.7%)	1 (3.4%)	369 (2.0%)	2 (11.8%)	738 (7.2%)	4 (11.4%)	1565 (10.4%)
Tui Chub	2 (7.7%)	1375 (9.3%)	9 (17.0%)	6137 (27.9%)	1 (4.8%)	471 (3.8%)	1 (3.4%)	732 (4.1%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Cyprinid spp.	1 (3.8%)	369 (2.5%)	6 (11.3%)	2385 (10.9%)	2 (9.5%)	1249 (10.0%)	1 (3.4%)	165 (0.9%)	0 (0.0%)	0 (0.0%)	3 (8.6%)	805 (5.3%)
Other	6 (23.1%)	1436 (9.7%)	13 (24.5%)	1708 (7.8%)	5 (23.8%)	927 (7.4%)	2 (6.9%)	774 (4.3%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Total[d]	26	14 844	53	21 964	21	12 495	29	18 035	17	10 296	35	15 101

[a] $\chi^2 = 5.18$, df = 4, $P = 0.27$.
[b] $\chi^2 = 5.65$, df = 4, $P = 0.23$.
[c] $\chi^2 = 1.55$, df = 2, $P = 0.46$.
[d] $\chi^2 = 4.88$, df = 4, $P = 0.30$.

Table 3. Number and percent of the seven most abundant fish species collected in Lake Britton by electrofishing and surface gill netting.

	Electrofishing				Surface Gill Netting	
	No.	%	Biomass (g)	%	No.	%
Tule Perch (*Hysterocarpus traski*)[a]	2130	38.8	25 705	3.6	27	12.0
Hardhead (*Mylopharodon conocephalus*)[a]	1120	20.4	80 921	11.2	125	55.6
Sacramento Sucker (*Catostomus occidentalis*)[a]	605	11.0	452 884	62.6	33	14.7
Sacramento Squawfish (*Ptychocheilus grandis*)[a]	588	10.7	68 796	9.5	19	8.4
Black Crappie (*Pomoxis nigromaculatus*)[b]	457	8.3	24 398	3.4	20	8.9
Bluegill (*Lepomis macrochirus*)[b]	322	5.9	3 614	0.5	0	0
Largemouth Bass (*Micropterus salmoides*)[b]	269	4.9	66 561	9.2	1	0.4
Total	5491	100.0	722 879	100.0	225	100.0

[a] Native species.
[b] Introduced species.

represented over 60% of the total biomass (Table 3). Sacramento Sucker, Hardhead, and Sacramento Squawfish together accounted for over 80% of the total fish biomass. Tule Perch, the most numerically abundant fish, comprised only 3.6% of the biomass samples. In the gill netting sample, suckers represented over 80% of the biomass.

Eagle prey selection at Britton Reservoir was significantly associated with fish abundance as indicated by gill netting data (Spearman rho = 0.626; $P < 0.05$) but not electrofishing data (Spearman rho = 0.191; $P < 0.10$). Ictalurids and Tui Chub were well represented in the eagles' diet but were rare in the electrofishing surveys (Vondracek et al. 1989). Conversely, Tule Perch, Largemouth Bass (*Micropterus salmoides*), and other centrarchids were abundant in the electrofishing surveys, but relatively unimportant to eagles. The relative percent of biomass of Hardhead and sucker in the diet was very similar to that in electrofishing; sucker and Hardhead comprised 73.8% of the 723 kg of fish sampled by electrofishing (Table 3) and averaged 73.5% of the eagles' diet.

Eagles nesting on the downstream portion of Britton Reservoir took fewer Sacramento Suckers than eagles nesting on the upstream section (Table 1). To evaluate the difference, we compared the relative abundance of Sacramento Sucker >200 mm, collected by electrofishing in upper and lower Britton Reservoir. We found that the upstream section contained more Sacramento Sucker >200 mm (19.1 per station; Vondracek et al. 1989) than the lower part of the reservoir (8.5 per station) where eagles relied more heavily on other species.

Foraging on the Small Reservoirs. Eagles nesting near the small downstream reservoirs took live fish and carrion fish (and waterfowl) in the reservoir bodies and inflow areas and dead and moribund fish emanating from the turbines of powerhouses situated on the reservoirs. Sacramento Sucker were the most abundant fish species both in terms of numbers and biomass identified in the downstream reservoirs (Reservoirs 4, 5, and 6) during electroshocking surveys. Hardhead, Sacramento Squawfish, and Tule Perch were also common. We saw eagles attempt to catch Hardhead and sucker near shore and in the main

Table 4. Habitat use by radio-tagged adult Bald Eagles nesting near riverine habitat as determined by radio-telemetry locations. Data include only the first detection of the day per location and exclude instances of soaring flight.

Territory	Sex	Reach 3	Reservoir 4	Reach 4	Reservoir 5	Reach 5	Tunnel Reservoir	Total Detections
Nest 7	Male	—	—	114 (17.2%)	271 (40.9%)	236 (35.7%)	41 (6.2%)	662
Nest 6	Male	1 (0.4%)	142 (64.3%)	78 (35.3%)	—	—	—	221
Nest 6	Female	0 (0.0%)	20 (38.5%)	32 (61.5%)	—	—	—	52

channels of reservoirs 4 and 5. At the upstream end of Reservoir 4, we frequently observed adults (Nest 6) taking suckers in the spring and summer in the currented shallows of an island gravel bar at the reservoir inflow where suckers were spawning. A backwater inlet at Reservoir 5 stranded several suckers on at least one occasion when water levels dropped.

We quantified habitat characteristics for 50 foraging attempts (60% successful) on the downstream reservoirs. Of these, 27 (54%) occurred in open water or flowing reservoir habitat, 13 (26%) in backwaters or marshes, 9 (18%) in powerhouse tailrace waters, and 1 (2%) unknown. Fourteen of 30 prey items appeared to be carrion. Tule Perch and crappie (*Pomoxis* sp.) carrion emerged from the powerhouse tailrace at Reservoir 4 primarily during winter and spring. Peaks in small carrion fish emerging from the tailrace into the reservoir corresponded with increased eagle attendance near the tailrace.

Bald Eagle Use of the River Sections. Bald Eagles that nested near the small reservoirs in the lower study area frequently perched and hunted along the river sections. In over half of 662 telemetry relocations of the radio-tagged adult male from Nest 7 (August 1983–February 1984 and May–December 1984) the eagle was in riverine habitats upstream and downstream of Reservoir 5 (Table 4). The total range was 22 river km.

Similarly, 35.7% of recorded relocations by the radio-tagged male at Nest 6 (6 June to 10 December 1984) were on the river rather than the reservoir. During 9 August to 30 September 1983, his mate perched mainly in riverine habitat (61.5% of relocations). Figure 3 shows that the ranges of the pair of radio-tagged adults at Nest 6 were very similar, both in extent (ca. 11 km) and distribution. Although the upstream river section (Reach 3) was just as accessible to the pair as the downstream reach (Reach 4), we observed the male in Reach 3 only once and

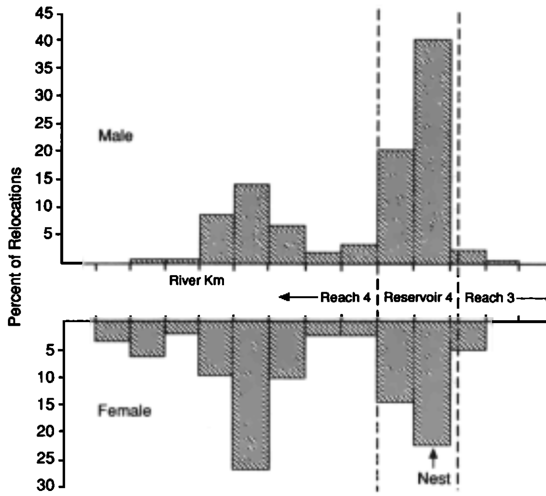

Figure 3. Home ranges of the adult pair of Bald Eagles at Nest 6 in the Pit River study as revealed by radiotelemetry.

Table 5. Mean number and biomass per hectare of the two major Bald Eagle prey species recorded in three riverine habitats on snorkel surveys of the Pit River in 1983 and 1984.

		HARDHEAD			SACRAMENTO SUCKER		
	NO. OF SURVEYS	NO.	BIOMASS (kg)	MEAN SIZE (g)	NO.	BIOMASS (kg)	MEAN SIZE (g)
Reach 3							
Pool	45	135.8	47.2	(347.6)	102.5	29.2	(284.9)
Run	40	7.1	2.1	(295.7)	345.5	23.0	(66.6)
Riffle	26	0.9	0.3	(333.3)	142.8	13.5	(94.5)
Reach 4							
Pool	12	57.8	23.2	(401.3)	138.0	100.9	(731.2)
Run	32	33.0	13.0	(393.9)	352.2	227.8	(646.8)
Riffle	25	12.9	2.0	(155.0)	443.2	279.5	(630.6)
Reach 5							
Pool	18	26.5	2.8	(105.7)	180.7	62.7	(346.9)
Run	34	55.6	12.4	(223.0)	447.0	133.6	(298.9)
Riffle	29	21.8	5.1	(233.9)	475.5	134.2	(282.2)

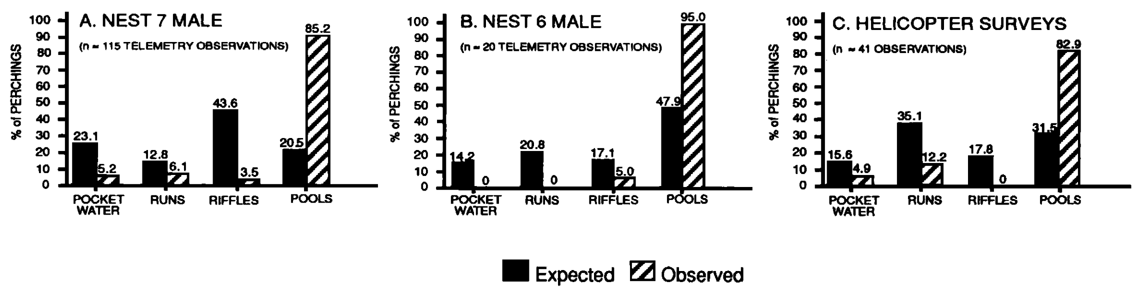

Figure 4. Observed and expected utilization of riverine habitats by Bald Eagles in Reaches 4 and 5. Graphs A and B show the expected percentages of telemetry observations of perchings in riverine habitats based on the proportional occurrence of each habitat within the home range of the eagle. For observations during helicopter surveys (C), percentages are based on habitat availability throughout Reaches 4 and 5.

the female never. In Reach 4 the ranges of the Nest 6 pair overlapped only slightly with that of the Nest 7 male.

Fish Occurrence in the River Reaches. Snorkeling surveys on the three river reaches (3, 4, and 5) provided data on the occurrence of Sacramento Sucker, Hardhead, Sacramento Squawfish, and Rainbow Trout (*Oncorhynchus mykiss*). Table 5 presents mean number and biomass per ha for sucker and Hardhead identified in the snorkeling surveys. Suckers were large and numerous in the riffles and runs of Reach 4, equally plentiful but smaller in Reach 5, and very small and least frequent in Reach 3. Conversely, Hardhead numbers were highest in Reach 3 pools, although they appeared larger in Reach 4. Trout numbers followed a similar pattern to Hardhead; they were more numerous in Reach 3 (especially riffles), intermediate in Reach 4, and fewest in Reach 5. Squawfish were most abundant in Reach 5 and intermediate in the other reaches; however, their numbers and biomass were comparatively low. We will later show an apparent connection between the distribution of these fishes, namely suckers, and the occurrence of foraging eagles.

Fish Behavior in the River Reaches. Our observations of fish behavior in Reach 4 showed that both Sacramento Sucker and Hardhead exhibited activity peaks during the morning. Suckers spent most of their active period slowly grazing on algae-covered cobble substrate. It was apparent that as they moved into the shallow areas (tails) of pools they came close enough to the surface to be caught by eagles. Their movement into pool tails may have also been related to spawning. Sacramento Suckers typically spawn in riffles (Moyle 1976), and in our study area riffles are usually preceded by pools. Therefore, suckers may pass though pool tails on their way to and from spawning areas.

Hardhead activity was variable. These sight feeders hovered in the middle of the water column and cruised along the river bank. We observed Hardhead feeding at the surface and in aquatic vegetation, browsing on the bottom, and apparently feeding on invertebrate drift in the water column. On two occasions, we observed eagles capture Hardhead swimming around beds of rooted aquatic vegetation. Hardhead feeding in this manner appeared to have their heads obscured by the plant material and appeared unaware of the eagle attack.

Riverine Habitat Selection. The riverine habitats used by the two radio-tracked male eagles (Nests 7 and 6) differed significantly from the proportional occurrence of aquatic habitats within their home ranges (Fig. 4). From 115 telemetry observations of the Nest 7 male, we recorded significantly more occurrences ($N = 98$, 85.2%) on river pool habitat than expected by chance ($\chi^2 = 297$, df = 3, $P < 0.001$). Similarly, in 20 river habitat observations of the Nest 6 male, he chose pools ($N = 19$, 95%) more often than expected by chance ($\chi^2 = 18.5$, $P < 0.001$). Helicopter surveys also showed eagles selecting pools disproportionately to pool occurrence ($\chi^2 = 94.9$, $P < 0.001$, 83% use in 34 of 41 observations compared to 31% availability; Fig. 4).

Foraging Behavior at River Pools. From blinds situated at riverine pools we noted that eagle attacks typically began high above the water from tree perches (20 of 25 observations); only one eagle struck without perching first. Attack distances ranged from 10 to 75 m. The success rate for all riverine forages observed from blinds was 16 in 25 attempts (64%), with 1 outcome undetermined. Exposed boulders were used as sites to drag and eat large fish. We identified the prey taken in ten instances: eight were Sacramento Sucker and two were Hardhead.

Water depth ranged from 0.1–1.26 m at 15 foraging strike points. Of 17 assessments of surface conditions in strike areas, only 2 showed a disturbance greater than swirls, whereas 11 had a glassy surface. The bottom was visible in 17 of 18 measurements of strike point turbidity; the exception showed visibility to a depth of 0.4 m. Water velocity at strike points was usually low; 7 of 16 observations showed no measurable current.

An analysis of river pool habitat characteristics and prey distribution at 11 pools indicated that eagle occurrence (total number of visits by telemetered eagles and eagles observed in helicopter surveys) was positively associated with the number of prey-sized fish per 100 m^2 (as determined by the snorkeling surveys, Pearson correlation coefficient, $r = 0.77$, $P < 0.01$). We also found a significant positive correlation of eagle occurrence with percent of pool area classified as "smooth/shallow" (no surface turbulence and <0.6 m deep, Pearson $r = 0.67$, $P < 0.03$). Comparisons of eagle occurrence with pool area, maximum depth of pool, percent algae coverage, length of pool tail (as a percent of pool length), and the total estimated number of prey fish per pool were not significant.

An experimental increase in flow above summertime conditions (4.2 m^3/sec) reduced the amount of shallow areas of no surface turbulence. The loss of smooth/shallow habitat for Reach 4 was quite high, with decreases for all seven pools averaging over 50% (minimum 27.6%, maximum 100%) at 8.5 m^3/sec flow. Water velocity in the studied pools generally increased with greater flows, but changes within smooth/shallow areas were inconsistent, with velocities both increasing and decreasing. Decreases in areas of no surface turbulence also resulted at each of the three pools measured in Reach 5 (minimum 7.2%, maximum 54.3%) when flows were increased from 2.8–4.2 m^3/sec.

Increased flows did not widen the river at most pools because of the relatively steep-sided canyon; therefore, availability of tree perches was not affected. Because pool length was dictated by hydraulic factors and did not change with flows, perch positions relative to pool boundaries did not change. However, increased flow reduced the number of exposed boulders at water level, which are often important to Bald Eagles as perches for manipulating heavy prey.

We caution the reader that specific management implications suggested by these results (i.e., managing for smooth/shallow habitat) may not apply to other river systems where Bald Eagles forage. Differing hydrologic and biotic factors may diversely influence the occurrence of catostomids and other prey fishes in pools, their activities within them, and their vulnerability to eagle attack. In Arizona, Hunt et al. (1992c) found pools least favored among the riverine habitats where Bald Eagles foraged on Desert Sucker (*Catostomus clarki*), Sonora Sucker (*C. insignis*), and Carp.

Eagle Distribution Versus Prey Occurrence. Based on the number of Bald Eagle sightings during helicopter surveys and the number and biomass of sucker per ha for six river segments (each river reach divided into upper and lower segments), eagle preference for the different river reaches was likely associated with the abundance of large suckers. The total number of eagle sightings in helicopter surveys were 1 and 5 for lower and upper Reach 3, respectively, and 24 for upper Reach 4. We saw eagles 15–18 times in each of the remaining segments.

The segments with the lowest eagle sightings also were estimated to have the lowest sucker populations (32.2 and 1.4 sucker per ha for lower and upper Reach 3, respectively). Upper Reach 4 had the largest sucker population (388.7/ha), the highest biomass (286.9 kg/ha) and the highest number of eagle sightings. The value for Spearman's rank correlation representing the correspondence between number of eagle sightings and biomass of suckers was 0.89 ($P < 0.05$). There was no significant correlation with numbers of suckers (rho = 0.77).

We reported above that the telemetered nesting pair of eagles at Reservoir 4 often foraged in the river section downstream of the reservoir (Reach 4), but rarely ventured upstream to the equally accessible Reach 3. Although suckers in size categories taken by these eagles (200–450 mm) were found in all habitats during snorkeling surveys of Reach 4 and electrofishing surveys of Reservoir 4, there were

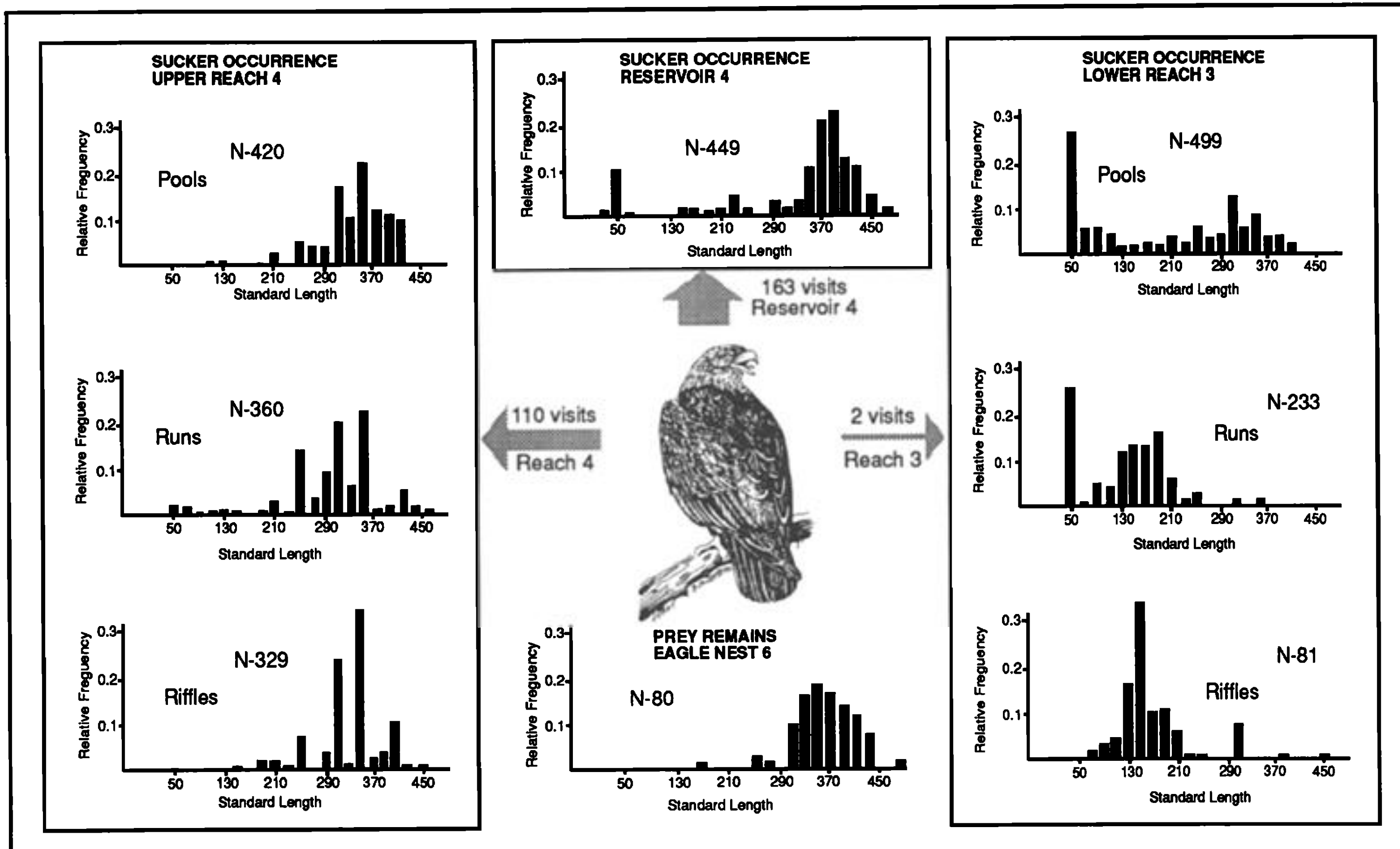

Figure 5. Relative length-frequency distributions of Sacramento Sucker in prey remains from Nest 6 compared with sucker length-frequencies observed in fish population surveys.

relatively few such fish observed in Reach 3 where smaller suckers were numerous (Fig. 5). Pools in upper Reach 4 contained four times the biomass of sucker per unit area (176.5 kg/ha) as lower Reach 3 pools (44.4 kg/ha). Sucker growth was limited in Reach 3 probably because of reduced algae growth and colder water than is optimum for suckers. Because of the diversion tunnel to the downstream powerhouse, Reach 3 was the only reach that did not receive relatively warm, nutrient-rich reservoir water in summertime.

DISCUSSION

Several points suggest a simple relationship between relative prey species abundance and prey selection. These points include the dominance of Sacramento Sucker in eagle diets in all parts of the study area, the increased use of other species in Lower Britton Reservoir where suckers were less common, the disproportionate use of pools with the highest densities of prey fish, and the rarity of eagle visits to Reach 3 where Sacramento Sucker of appropriate body size were in relatively low density.

Our data also show how prey behavior and life history can influence vulnerability to predation. Sacramento Sucker were not only numerous, they were also vulnerable to eagles in more ways than other species. They became available when they: 1) foraged in shallow water, 2) spawned in shallows, and 3) appeared as carrion. The first two components of vulnerability, characteristic of many catostomids, no doubt account for their occurrence in the diets of Bald Eagles over much of their inland range (Dunstan and Harper 1975, Todd et al. 1982, Swenson et al. 1986, Haywood and Ohmart 1986, Gerrard and Bortolotti 1988, Hunt et al. 1992c). Not only do suckers typically enter shallow water to spawn and graze (photosynthesis is highest in shallow habitats), but their downward visual orientation must leave them more vulnerable to eagle attack than sight-feeding fish (see Swenson 1979, Todd et al. 1982 for discussion). This point helps to explain the apparent contradiction of a bottom-feeding fish being the major prey of a surface-feeding predator (Haywood and Ohmart 1986). Accordingly, sight-feeding cyprinids (Hardhead and Sacramento Squawfish) appeared in significantly less frequency in prey remains than predicted by their occurrence relative to Sacramento Sucker in the gill netting and electroshocking samples on Britton Reservoir (Tables 1 and 3). Trout, also sight-feeders, were common in the river reaches, but were rarely taken by eagles. Both Hardhead and trout often wait near the surface for insects, but these fish tend to be oriented upward and are more aware than suckers of any movement above them.

We believe the timing and occurrence of sucker mortalities on Britton Reservoir may contribute to the unusually high nesting density of Bald Eagles there. This carrion "bloom" coincides with the second half of the nestling cycle, including the post-fledging period. Large post-spawning dieoffs are atypical among catostomids, and P.B. Moyle (pers. comm.) believes that the proportion of the total sucker spawners dying each year as a result of spawning stress is small. However, dead and dying fish, drifting down from the relatively long river reach upstream, tend to accumulate in the reservoir inflow area where they are highly visible to the eagles. Carrion fish may also be produced by stranding as a result of flow variation from the powerhouse upstream of the reservoir.

Another point of difference between eagle diet and species occurrence in the fisheries inventories involved ictalurids. Bullheads (*Ictalurus melas* or *I. nebulosus*) were absent in the extensive electrofishing, gill netting, and carrion survey samples on Britton Reservoir, and yet we identified 123 individuals in eagle prey remains (Table 1). Dunstan and Harper (1975) and Van Daele and Van Daele (1982) mention that bullheads often swim or "bask" near the surface, and indeed, we witnessed unidentified ictalurids doing so on Britton Reservoir. How they avoided the gill nets is unknown to us.

Finally, although relative eagle use of the three river reaches was directly related to the abundance of large suckers (>200 mm), our data show that physical conditions promoting prey vulnerability were more important in attracting foraging eagles to specific habitats than were factors influencing prey density. Eagles chose river pool habitat despite the fact that sucker densities in Reaches 4 and 5 were invariably lower in pools than in runs or riffles, and there were no consistent size-class differences of suckers between the three habitats (Table 5).

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