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BALD EAGLE FORAGING AND RESERVOIR MANAGEMENT IN NORTHERN CALIFORNIA

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ABSTRACT.—We studied food habits, mechanisms of prey acquisition, and the effects of reservoir drawdown and fisheries management in a population of Bald Eagles (*Haliaeetus leucocephalus*) nesting on Shasta (Lake) Reservoir, a large impoundment in northern California used intensively for irrigation and recreation. Prey deliveries at seven nests were mostly bass (*Micropterus* sp., 55% of total prey biomass) and salmonids (14%), and all principal fish prey species were either introduced or regularly stocked. Carrion and moribund fish, mostly bass, accounted for >75% of successful foraging attempts. Fish mortality was related to spawning stress, disease, and catch-and-release angling; fish fatalities associated with bass fishing provided carrion throughout the breeding season. The proportions of fish species in the eagles' diet, as measured by prey deliveries to the nest, were positively correlated with those found in live-fish sampling and carrion surveys; all were predominantly bass. Benefits associated with seasonal and long-term reservoir drawdown included exposing spawning and foraging fish to eagle predation, and the likely release of nutrients and food for rapid fish growth upon re-inundation. Probable disadvantages of extended drawdown included loss of eagle foraging habitat and reductions in the standing crop of fish, likely resulting in competition among eagle pairs. Bald Eagle productivity was at or above average during the 2-yr study, a relatively wet period following a long drought and associated low pool levels, and we found a positive relationship between historic spring reservoir levels and Bald Eagle productivity from 1979–1999. Effects of fish introductions on trophic relationships and species composition warrant careful examination of eagle foraging requirements; however, past and present fisheries management appears to be currently benefiting the opportunistic eagles.

KEY WORDS: *Bald Eagle*, *Haliaeetus leucocephalus*; *California*; *food habits*; *foraging ecology*; *reservoir management*.

FORRAJEJO DE *HALIAEETUS LEUCOCEPHALUS* Y MANEJO DE UNA REPRESA EN EL NORTE DE CALIFORNIA

RESUMEN.—Estudiamos los hábitos de alimentación, los mecanismos de adquisición de presas, y los efectos del vaciado de una represa y del manejo de la pesca en una población de *Haliaeetus leucocephalus* que nidifica en la Represa (Lago) Shasta, un gran reservorio en el norte de California usado intensivamente para riego y recreación. Las presas entregadas en siete nidos fueron en su mayoría peces del género *Micropterus* (55% del total de la biomasa de las presas) y salmónidos (14%). Además las principales especies de peces presa fueron todas introducidas o sembradas con regularidad. La carroña y los peces moribundos, principalmente *Micropterus* sp., representaron más del 75% de los intentos exitosos de forrajeo. La mortalidad de peces se relacionó con el estrés de la puesta de huevos, con enfermedades y con la pesca del tipo captura y posterior liberación; la muerte de peces asociada con la pesca de *Micropterus* sp. produjo carroña a lo largo de la estación de cría. Las proporciones de especies de peces en la dieta de las águilas, medida como las presas entregadas al nido, estuvieron positivamente correlacionadas con aquellas encontradas en

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muestras de peces vivos y en muestreos de carroña; todas las muestras consistieron en su mayoría de *Micropterus* sp. Los beneficios asociados con el vaciado estacional y a largo plazo de la represa incluyeron la exposición a la depredación por parte de las águilas, de peces que se encuentran desovando y forrajeando, y la probable liberación de nutrientes y alimentos para el crecimiento rápido de peces durante la inundación subsiguiente. Las desventajas probables de períodos extendidos de aguas bajas incluyeron la pérdida de hábitat de forrajeo para las águilas y la reducción en los volúmenes disponibles de peces, provocando probablemente la competencia entre parejas de águilas. La productividad de *H. leucocephalus* fue similar o superior al promedio durante los dos años de estudio, un período relativamente húmedo que siguió a una larga sequía y a bajos niveles de agua de la represa. Encontramos una relación positiva entre los niveles de primavera históricos de la represa y la productividad de *H. leucocephalus* entre los años 1979 y 1999. Los efectos de la introducción de peces en las relaciones tróficas y en la composición de especies ameritan un examen cuidadoso de los requerimientos de forrajeo de las águilas. Sin embargo, el manejo durante el pasado y el presente de las pesquerías parece estar beneficiando actualmente a estas águilas oportunistas.

[Traducción del equipo editorial]

Despite blocking hundreds of miles of Pacific salmon (*Oncorhynchus* spp.) spawning habitat, the construction of reservoirs in California provided Bald Eagles (*Haliaeetus leucocephalus*) with habitat for expansion following their decline mid-century from degradation of historical nesting habitat and DDT poisoning, especially in marine environments (Detrich 1989). Therefore the management of large reservoirs is of interest for eagle conservation, as is the study of the effects of irrigation, hydroelectric power, and recreational demands. Reservoir fluctuations and releases often compromise riparian habitats and populations of aquatic or wetland species. Although nonnative fish commonly are introduced to reservoirs to increase opportunities for anglers, there are questions regarding their suitability for eagle foraging and their effects on native fish.

Reservoir characteristics affect fish species composition and prey availability for nesting Bald Eagles (Hunt et al. 1992, Hunt et al. 2002). Operations of narrow, run-of-the-river (i.e., minimal flooding behind dam) hydroelectric reservoirs in northern California favor native Sacramento suckers (*Catostomus occidentalis*), the resident eagles' principle prey, while discouraging populations of introduced centrarchids (sunfish; Centrarchidae) such as bass species (*Micropterus* spp.; Vondracek et al. 1989). In contrast, at irrigation storage reservoirs in Arizona, nonnative warm-water fish species such as catfish (Ictaluridae), common carp (*Cyprinus carpio*), bass, and crappie (*Pomoxis* sp.) flourished and became available to Bald Eagles as abundant carrion following spawning (Hunt et al. 2002). Little is known about the effects of seasonal and extended drawdown of reservoirs on Bald Eagle foraging.

The primary goals of this study were to quantify the diet of a population of breeding Bald Eagles on

Shasta Reservoir, inventory important prey species to compare their abundance with use by eagles, and determine how prey fish become available to eagle capture throughout the breeding season (i.e., alive or as carrion) and under what conditions (e.g., as post-spawn fatalities). We also explore how fisheries management and seasonal and multiple-year drawdowns of reservoir pool level affect availability of prey species and Bald Eagle foraging in 2 yr of differing conditions.

METHODS

Study Area. Shasta (Lake) Reservoir, located 16 km north of Redding, California in Shasta County, was created in the 1940s with the construction of Shasta Dam. The largest human-made reservoir in California, it impounds several major tributaries including the Sacramento, McCloud, and Pit rivers. At full pool elevation above sea level (ASL; 325 m) the reservoir covers approximately 120.5 km² and holds 555 000 hectare-meters of water. Typical reservoir operations are summer drawdown for Central Valley irrigation needs and for preparation for flood control in winter, and gradual late winter to spring storage increases to near full pool if possible. Terrestrial habitats are a mix of lower montane coniferous forest dominated by ponderosa pine (*Pinus ponderosa*), cismontane woodlands dominated by oaks (*Quercus* spp.) and ponderosa and foothill pines (*P. sabiniana*), and chaparral dominated by manzanita (*Arctostaphylos* spp.) and ceanothus (*Ceanothus* spp.).

Our study period did not include a drought year with extremely low reservoir levels; however, the conditions between the two field seasons differed. In 1998, May and June rains increased water levels and cool temperatures prevailed until late in the eagles' nesting cycle. In 1999, warmer temperatures combined with earlier reservoir drawdown. Reservoir level peaked at 2.3 m higher and 29 d later in 1998 (19 June) than 1999 (21 May), and by late July was 4.8 m higher in 1998 compared to 1999.

Diet. We analyzed prey remains collected at a total of 17 unique ($N = 16$ in 1998 and $N = 13$ in 1999) active nests (i.e., nests where eggs had been laid), and conducted di-

rect observations of prey deliveries at seven of these nests. Prey remains were collected in and below nests in late May or early June when nestlings were approximately 8 wk old and again in late July after fledging of young in 1998 and 1999. A sample of nest lining was collected for identification of scales. Prey were identified and biomass estimated per Jackman et al. (1999).

To overcome problems associated with underestimation of small, soft-boned fish (e.g., trout [Salmonidae]) and overrepresentation of large, bony fish (e.g., carp, catfish) and birds (Todd et al. 1982, Knight et al. 1990, Grubb 1995), we established observation points on hillsides above nests and identified prey items brought to the nest using a high-powered telescope. Distances from observation points to nests ranged from 150–500 m; at closer sites, vegetation and makeshift blinds hid the observer from eagles. We also recorded the estimated size (based on comparison to the approximate size of eagles' feet or culmen) and status (e.g., alive or carrion) of each prey item.

Foraging. We studied the foraging behavior of eagles at seven territories: four in 1998 and three others in 1999. We visited each site for 2–3 d consecutively every 2 wk from early April through July, beginning observations approximately 0.5 hr before sunrise and observing until noon. We followed one or both of the adults by boat during foraging flights and later collected habitat data at foraging locations.

At each foraging strike point, we measured water temperature, water depth, capture technique [i.e., active foraging (on live prey), scavenging, piracy] distance from shore, water clarity (Secchi disc), reservoir level, and prey status. Piracies involved taking food in the air from Osprey (*Pandion haliaetus*; Osprey piracy), other eagles (eagle piracy), or on shore from any scavenger (scavenge-piracy). A shore-scavenge occurred on carrion taken or eaten on shore. Prey status (i.e., live, moribund, or carrion) was determined by capture mode and prey movement. Carrion fish were limp and typically plucked from the water by the eagle at the terminus of a direct flight (scavenge-pluck). Live fish, bright and usually animated upon capture, were obtained with a more active flight pattern sometime including multiple passes (active foraging). This often followed a period of obvious visual assessment from a low perch, in contrast to carrion retrieval which typically followed scanning of the reservoir from a higher perch or a search on the wing. We suspect that some moribund fish were likely mistaken as either live or carrion depending on the degree of mobility. We observed moribund fish dying at the surface that sometimes dove when approached by boat, eventually returning to the surface, where they were often retrieved by eagles.

To facilitate our observations of foraging eagles, we radiotagged the adult males at territories where direct observation was difficult, such as near narrow canyon inflow areas. We employed the floating noosed fish techniques described in Cain and Hodges (1989), and Jackman et al. (1993). Other pairs in open-water territories were relatively easy to follow visually and did not require telemetry. We measured beak depth and halux length to determine sex (Bortolotti 1984), and attached a 3-yr, 60-gm VHF (Bio-track Ltd., Wareham, Dorset, U.K.) transmitter backpack using teflon-coated nylon straps connected at the sternum with cotton embroidery thread.

Prey Base. We sampled prey fish abundance by inventorying fish populations and by conducting biweekly carrion surveys in seven territories. We established electroshocking stations, gillnetting stations, and snorkeling transects in varied shoreline habitats within these territories during spring. We used an electrofishing boat at 50-m shoreline sampling stations during the early morning hours. Gillnets were 2 m × 100 m, variable-mesh monofilament nets placed overnight perpendicular to shore and suspended at or as near the surface as possible. Captured fish were identified to species, measured, and released. Along 100-m snorkeling transects, three snorkelers swam parallel in shallow to deep (approx. 5 m) littoral habitats and recorded numbers and species of fish by size class onto diving slates. Only individuals >100 mm total length (TL) were used in the fisheries analysis.

Carrion surveys were conducted biweekly; each survey consisted of three separate 1-km-long shoreline boat transects per territory. The surveys included various habitats (e.g., coves, shallow muddy flats, steep rocky shorelines) where prevailing currents and winds were likely to concentrate floating debris. Data collected on each carrion item included location, position (e.g., on shore, open water), species, length, condition (fresh, putrid, partially consumed), and notes on possible causes of death (wounds, fungal patches, etc.). Additional carrion occurrences were also recorded during eagle foraging observation sessions.

Data Analyses. To evaluate whether Bald Eagle use of foraging habitats, available prey base, and captured prey species was consistent between years, we compared pooled data from the territories studied in 1998 with those studied in 1999. Low sample size at some territories and for some fish species did not allow between-territory data comparisons. We used the Yates correction for chi-square tests of differences between distributions with one degree of freedom. In evaluating differences between means of foraging habitat parameters, nonnormal data were treated with the Wilcoxon rank sum test; normally distributed data were compared with a *t*-test. Using pooled data from both years, we ranked fish species' occurrences within appropriate taxonomic groups and used Spearman's rank correlation to test for correlation between Bald Eagle diet (prey deliveries and prey remains, separately), prey abundance (fisheries), and prey availability (carrion). Data from all fisheries sampling techniques were pooled in computing relative abundance of prey fish for this analysis by combining unweighted numbers of appropriate size fish for each species group observed or collected during snorkeling, electrofishing, and gillnetting.

Mean spring reservoir pool elevation (MSPE) was calculated by averaging mean monthly elevation data (m ASL; U.S. Bureau of Reclamation unpubl. data) for March, April, and May for each year from 1979–1999. Reproductive data were collected during primarily boat surveys conducted typically three times per year (February, April, and June; U.S. Forest Service unpubl. data). Occupied territories were defined as those where two adults were observed in or near a nest during surveys, or where at least one adult was observed incubating or with young. Annual Bald Eagle productivity (young per occupied nest site) was determined by dividing the total number of young counted in the final survey by the total number of occupied nest sites.

Table 1. Number of individuals and estimated biomass (kg) of prey identified from remains collected in and below 17 Bald Eagle nests on Shasta Reservoir, California, 1998 and 1999.

PREY CATEGORY	NUMBER (%)	BIOMASS (%)
Fish (Osteichthyes)		
Bass (<i>Micropterus</i> spp.) ^a	153 (34.2)	77.2 (14.2)
Catfish (Ictaluridae) ^b	102 (22.8)	121.4 (22.4)
Common carp (<i>Cyprinus carpio</i>)	71 (15.9)	244.4 (45.1)
Trout/salmon (Salmonidae) ^c	17 (3.8)	16.1 (3.0)
Crappie (<i>Pomoxis</i> spp.)	13 (2.9)	3.1 (0.6)
Sacramento sucker (<i>Catostomus occidentalis</i>)	6 (1.3)	5.6 (1.0)
Native minnows (Cyprinidae) ^d	2 (0.4)	2.1 (0.4)
Fish subtotal	364 (81.4)	469.9 (86.7)
Birds (Aves)		
Dabbling ducks (<i>Anas</i> spp.)	31 (6.9)	20.6 (3.8)
American Coot (<i>Fulica americana</i>)	12 (2.7)	6.9 (1.3)
Goose spp. (Anserinae)	8 (1.8)	22.3 (4.1)
Other birds	28 (6.3)	18.2 (3.4)
Bird subtotal	79 (17.7)	68.0 (12.6)
Mammals (Mammalia)		
Black-tailed jackrabbit (<i>Lepus californicus</i>)	2 (0.4)	2.8 (0.5)
Squirrels (Sciuridae)	2 (0.4)	1.4 (0.2)
Mammal subtotal	4 (0.9)	4.1 (0.7)
Total prey items	447 (100.0)	542.0 (100.0)

^a Includes at least 34 spotted bass (*Micropterus punctulatus*), two largemouth bass (*M. salmoides*), and one smallmouth bass (*M. dolomieu*).

^b Includes at least 71 channel catfish (*Ictalurus punctatus*), 21 white catfish (*Ameiurus catus*), and two brown bullhead (*A. nebulosus*).

^c Includes at least two rainbow trout (*Oncorhynchus mykiss*).

^d Includes one hardhead (*Mylopharodon conocephalus*) and one Sacramento pikeminnow (*Ptychocheilus grandis*).

RESULTS

Bald Eagle Diet. Bass were the most numerous species identified in eagle prey remains, followed by catfish species and common carp (Table 1). However, this order was reversed for relative biomass contributions, with carp providing >45% of biomass. Bass were the only prey species present in all 17 nest site collections. Very few native fishes (i.e., suckers, minnows [Cyprinidae]) were found. Birds, particularly waterfowl, and some mammals were also represented.

Fresh catfish bones ($N = 5$) were infrequent in all nest prey collections in early June 1998, a period representing the early part of the nesting cycle, whereas catfish were considerably more numerous ($N = 27$) in the post-fledging collections in August 1998. In 1999, a reverse trend was evident ($N = 12$ early, $N = 5$ late; $\chi^2 = 12.47$, 1 df, $P = 0.0004$).

Observation of prey deliveries at seven nests provided an assessment of diet without the biases associated with analyses of prey remains. Bass accounted for the majority of deliveries and also represented the bulk of biomass delivered at all sites combined (Table 2). In addition, bass were the only fish spe-

cies brought to all seven nests. The frequency distributions of three fish groups (i.e., bass, salmonids [Salmonidae], and all other fish) were similar for all deliveries recorded in 1998 compared to those in 1999 ($\chi^2 = 1.75$, df = 2, $P = 0.42$).

Foraging Behavior. We observed 140 foraging events during the 1998 field season and 121 during 1999. For both seasons combined, eagles were successful in 80% of 261 attempts at prey (Table 3). Success rates were similar between 1998 and 1999 for fish (84%–102 of 122 attempts in 1998, 83%–99 of 119 attempts in 1999; $\chi^2 = 0.01$, df = 1, $P = 0.94$). The proportions of fish captures classified as carrion, live, moribund, or piracies were also statistically indistinguishable between the 2 yr ($\chi^2 = 4.64$, df = 3, $P = 0.20$).

The most common eagle hunting technique consisted of a scavenge-pluck of carrion fish from the surface of the reservoir. Carrion and moribund fish accounted for >75% of successful foraging attempts on Shasta Reservoir.

Eagles caught 5 of 17 (29%) live birds they attempted to capture, all in the early nesting season, and 13 of 26 live fish (50% success). Live fish were

Table 2. Number of individuals and estimated biomass (kg) of prey identified from prey deliveries to seven Bald Eagle nests at Shasta Reservoir, California, 1998 and 1999. Data exclude four unidentified fish.

PREY CATEGORY	NUMBER (%)	BIOMASS (%)
Fish		
Bass ^a	61 (64.9)	20.5 (54.6)
Salmonids ^b	12 (12.8)	5.3 (14.2)
Catfish ^c	5 (5.3)	1.6 (4.2)
Other Centrarchids ^d	5 (5.3)	1.2 (3.2)
Common carp	4 (4.3)	5.2 (13.8)
Threadfin shad (<i>Dorosoma petenense</i>)	1 (1.1)	(tr.) (tr.)
Fish subtotal	88 (93.6)	33.8 (90.0)
Birds		
American Coot	4 (4.3)	2.1 (5.5)
Cinnamon Teal	1 (1.1)	0.3 (0.9)
Common Merganser	1 (1.1)	1.3 (3.5)
Bird subtotal	6 (6.4)	3.8 (10.0)
Total prey items	94 (100.0)	37.6 (100.0)

^a Includes at least 17 spotted bass and one smallmouth bass.

^b Includes at least 3 rainbow trout and one chinook salmon.

^c Includes at least one channel catfish and one white catfish.

^d Includes at least two crappie sp.

Table 3. Characteristics of Bald Eagle foraging activity observed on Shasta Reservoir during April–July 1998 and 1999. Capture modes and prey status were not observed/recorded for all foraging attempts.

	ALL ATTEMPTS		SUCCESSFUL ATTEMPTS	
	N	%	N	%
Prey type				
Fish	241	92	201	96
Bird	18	7	6	3
Mammal	1	<1	1	<1
Reptile	1	<1	1	<1
Totals	261	100	209	100
Fish capture technique				
Scavenge-pluck	111	49	102	55
Active foraging	42	19	28	15
Osprey piracy	36	16	23	12
Shore-scavenge	25	11	23	12
Eagle piracy	5	2	5	3
Scavenge-piracy	4	2	4	2
Aborted attempt	2	1	0	0
Totals	225	100	185	100
Fish status				
Dead (carrion)	130	61	123	69
Captured ^a	41	19	28	16
Alive	26	12	13	7
Moribund (dying)	15	7	14	8
Totals	212	100	178	100

^a Piracy attempt against osprey (88%) or eagle (12%) with a captured fish.

Table 4. Aquatic habitat characteristics (mean \pm SE) measured at Bald Eagle foraging strike points for various prey status types on Shasta Reservoir, California, 1998 and 1999.

FORAGING HABITAT PARAMETER	PREY STATUS	1998 (N)	1999 (N)	P	1998–1999 POOLED (N)
Distance to shore (m)	carriion	61 \pm 11 (71)	60 \pm 13 (65)	0.14 ^a	61 \pm 8 (136)
Distance to shore (m)	alive	7 \pm 2 (10)	8 \pm 3 (5)	0.69 ^a	7 \pm 2 (15)
Distance to shore (m)	pirated	160 \pm 49 (10)	135 \pm 47 (13)	0.26 ^a	146 \pm 35 (23)
Water depth (m)	carriion	22.8 \pm 3.0 (57)	20.1 \pm 2.8 (50)	0.53 ^b	21.5 \pm 2.0 (107)
Water depth (m)	live	9.5 \pm 2.9 (8)	8.5 \pm 3.6 (4)	0.83 ^a	9.1 \pm 2.4 (12)

^a Between-year comparisons (P) for Wilcoxon rank sum test.

^b Between-year comparisons (P) for t-test.

taken while feeding, basking, or spawning at the surface or in shallow water. During reservoir draw-down, eagles targeted channel catfish (*Ictalurus punctatus*) protecting nest cavities around stumps, and bass feeding around exposed brush piles.

Attempts to pirate Osprey carrying fish were mostly successful (64% success; Table 3). Bald Eagle pairs with nests that were located <1.6 km from two or more active Osprey nests ($N = 5$ pairs) foraged more often by attempting Osprey piracy (34 of 204 foraging attempts) than pairs >1.6 km from multiple active Osprey nests ($N = 2$ pairs; 2 of 55 foraging attempts; $\chi^2 = 5.04$, $df = 1$, $P = 0.02$). Osprey provided eagles greater access to salmonids: 7 of 14 fish pirated from Ospreys were identified as salmonids, and 11 of 80 fish obtained by other foraging techniques were salmonids ($\chi^2 = 7.79$, 1 df , $P = 0.005$).

Foraging Habitats. Measurements of foraging habitat parameters were similar between years (Table 4). Data for live fish suggested that eagles tended to catch them within 10 m of shore (73%, $N = 11$), and that water depth at most of these locations was >2 m (75%, $N = 9$). Almost half of the carriion retrievals occurred near shore (0–10 m; 49%, $N = 67$); however, most were in relatively deep water. All measurements of water clarity were greater than 50 cm, or were clear to the bottom.

Eagle foraging in tributaries upstream of the reservoir was confirmed for one radio-tagged adult at only one territory. The eagle captured spawning Sacramento pikeminnow (*Ptychocheilus grandis*), a native cyprinid, at the inflow to the reservoir.

Prey Base. Biweekly carriion surveys yielded varied numbers of carriion fish (0.13 to 1.64 fish items/survey/territory). We found bass carriion during all months, but it and other centrarchid carriion (mostly crappie) peaked in May when water temperatures

were optimum for spawning. Bass (89% spotted bass [*Micropterus punctulatus*]) were the only fish found as carriion at all seven territories during surveys. The frequency distribution of three groups, bass, salmonids, and all other fish species combined, was similar in 1998 and 1999 ($\chi^2 = 1.75$, $df = 2$, $P = 0.41$).

Although we were unable to assess the cause of death for most carriion scavenged by eagles, our observations of fish carriion found on the reservoir indicated multiple sources. Some carriion bass and crappie showed obvious signs of spawning stress (i.e., gametes [ova, milt] still emerging from fresh carcasses). Many fish and especially bass were diseased, including bacterial infections from Columnaris disease (*Flexibacter columnaris*) and fungal infections from Saprolegniasis (*Saprolegnia* sp.). These were noted at the sites of probable hook wounds from catch-and-release anglers, at caudal fins possibly abraded when fanning bottom substrate at nest sites, and other areas. Carriion threadfin shad (*Dorosoma petenense*) showed signs of wounding from attacks by predatory fish. Acid mine drainage with copper contamination at three tributary inlets asphyxiated salmonids seeking the cold water inflow, a factor that eagles exploited.

Mortality factors determined from examining carriion fish items are summarized in Table 5. Angler wounds were represented by hook wounds, tackle still attached, and filleted carcasses. One bass died with a crappie obstructing its mouth. Salmonid carriion peaked in April as a result of the mine poisoning and stocking fatalities.

Bass were the most common fish found during fisheries sampling in Bald Eagle territories. Bass (93% spotted bass) accounted for 88% of total fish numbers ($N = 323$), followed by other sunfish (6%), salmonids (3%), channel catfish (2%), and carp (1%). Bass were the only fish common to samples

Table 5. Summary of carrion and moribund fish items found on Shasta Reservoir in 1998 and 1999, and apparent causes of death if known. Unknowns were either decomposed or fresh with no obvious wounds or signs of spawning (i.e., emerging eggs or milt).

PREY CATEGORY	TOTAL NUMBER	OBSERVED MORTALITY CAUSES				
		DISEASE	SPAWNING STRESS	ANGLER WOUNDS	OTHER	UNKNOWN
Bass ^a	78	24	2	11	1	40
Other Centrarchids ^b	12	4	2	1	0	5
Salmonids ^c	10	4	0	0	1	5
Common carp	7	1	1	1	0	4
Catfish ^d	6	2	0	0	0	4

^a Includes 65 spotted bass, eight smallmouth bass, and five largemouth bass.

^b Includes seven crappie and five bluegill (*Lepomis macrochirus*).

^c Includes at least four rainbow trout and four chinook salmon (*Oncorhynchus tshawytscha*).

^d Includes four channel catfish, one white catfish, and one brown bullhead.

at all territories, and the numbers of bass compared to all other fish combined were distributed similarly in 1998 and 1999 ($\chi^2 = 1.87$, $df = 1$, $P = 0.17$).

Fish Prey Use vs. Species Abundance. Bass were the dominant species group overall in eagle diets, carrion surveys, and fish sampling and, with a few exceptions, all other fish species represented only minor components (Fig. 1). Catfish and carp were more prominent in the prey remains due to their heavy-boned characteristics. Salmonid numbers

were low in the prey remains probably because their soft bones are often completely consumed by eagles; only scales were evident in some nests.

The frequencies of each species group identified in prey deliveries (Fig. 1) were positively correlated with those found in fisheries sampling (Spearman $r_s = 0.93$, $P < 0.01$) and carrion surveys ($r_s = 0.88$, $P < 0.05$). Also, the frequencies of species found during carrion surveys were positively correlated with those from the fisheries sampling ($r_s = 0.92$, $P < 0.02$),

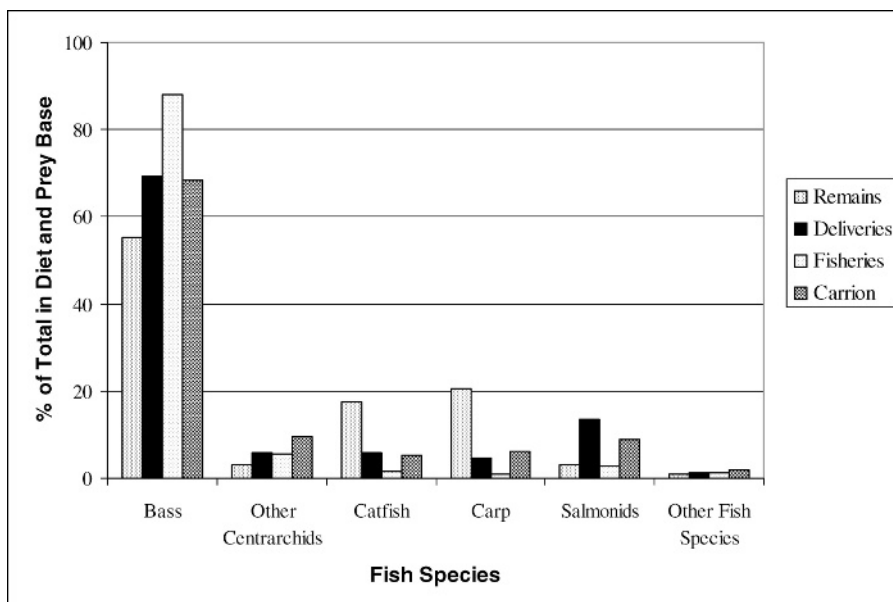


Figure 1. Bald Eagle fish diet (species frequencies) identified from prey remains and deliveries, compared to prey base frequencies identified from fisheries sampling and carrion counts, Shasta Reservoir, California.

implying that fish died in proportion to their numbers. Frequencies of fish species found in the prey remains from the seven territories were not correlated with those of prey deliveries (Spearman $r_s = 0.67$, $P > 0.05$), fisheries sampling ($r_s = 0.55$, $P > 0.05$), or carrion surveys ($r_s = 0.70$, $P > 0.05$).

Reservoir Levels and Productivity. There were eight occupied nesting territories on Shasta Reservoir in 1979, increasing to 19 in 1999; most of the increase occurred during the mid- to late 1990s. A weak, positive relationship existed between mean spring (March–May) reservoir pool elevation (MSPE, in m) and Bald Eagle productivity (young per occupied site [YOS]) on Shasta Reservoir from 1979 to 1999 (simple linear regression $r^2 = 0.25$, $F = 6.33$, $P = 0.02$; $YOS = -5.0624 + 0.0188 * MSPE$), a period that included extended years of drought with very low reservoir levels (1988–1992).

DISCUSSION

The opportunistic nature of foraging Bald Eagles is well documented (Buehler 2000). It is noteworthy, therefore, that most comparisons of foraging habitat and prey metrics in our study were statistically indistinguishable between study years. This level of uniformity, despite somewhat different reservoir conditions and some examples of foraging opportunism unique to territories and each year of study, revealed a clear preference by breeding eagles for the relatively easy acquisition of carrion, especially bass, on Shasta Reservoir.

Fisheries. We identified disease as a primary cause of bass fatalities, exacerbated by spawning stress and angler handling. The two pathogens are often fatal, and both are associated with stress, crowding, and trauma (Sullivan 1975). Such conditions are encountered in the wild during spawning, when energy resources are strained and when fins are abraded building nests, and in connection with anglers, who hook, handle, and confine fish in crowded live wells, especially during tournaments.

Unlike some other perciforms whose spawning created brief carrion “blooms” (e.g., yellow perch [*Morone mississippiensis*] Hunt et al. 2002), the availability of spotted bass carcasses at Shasta Reservoir was prolonged. They were present from April through July and peaked in May during optimal water temperatures for bass spawning (15–17°C). However, the most significant factor affecting the availability of bass carrion throughout the rest of summer was likely anglers, especially those practicing catch-and-release fishing. Although we did not attempt to quantify the

extent to which bass fishing and tournaments contributed to carrion production at Shasta Reservoir, delayed mortality estimates for handled fish have been reported to be >30% from tournaments elsewhere (Meals and Miranda 1994, Steeger et al. 1994). Tournaments on Shasta Reservoir often lasted 2–3 d and included hundreds of anglers.

Bald eagles also retrieved fish carcasses that had been filleted by fishermen, and we found numerous fishing lures and monofilament fishing line in nests and below nest sites, presumably from fish that had broken off lines and later died of injuries. A potential disadvantage to this food source is the chance that nestlings or adults might become entangled in lines or impaled with fishing hooks (Driscoll et al. 1999).

Every year thousands of hatchery salmonids are released into Shasta Reservoir. As many as 20% of the hatchery trout die soon after release, and many initially inhabit the top of the water column because of increased oxygen levels there (H. Rectenwald pers. comm.). Columnaris disease infects some individuals starting at the hatchery, because the crowded conditions in live wells often damage their protective mucus layer.

Catfish require warm water temperatures to initiate spawning (>21°C for channel and white catfish [*Ameiurus catus*]). Surface temperatures reached 21°C in late June 1998 and in late May 1999 during our study. Based on our comparison of prey remain collections at nests, more catfish were taken by eagles earlier in 1999 than in the previous year when water temperatures were cooler, suggesting an association with spawning activity.

Fish introductions in Shasta Reservoir have affected trophic levels, and nonnative spotted bass have evidently replaced Sacramento blackfish (*Orthodon microlepidotus*) in the eagles' diet. During the 1980s, 38% of prey (by biomass) of nesting eagles was native cyprinids, mostly blackfish (Jackman et al. 1999), but this species apparently no longer occurs in the reservoir (N. Mangi pers. comm.). Their demise coincided with the introduction and proliferation of the spotted bass, an efficient predator of juvenile fish, and the 7-yr drought of the late 1980s and early 1990s.

Other Prey Sources. Osprey numbers increased on Shasta Reservoir from 17 pairs in 1982 to over 70 pairs in 1998 (U.S. Forest Service unpubl. data). Osprey helped expand the Bald Eagle feeding niche, as eagles pirated fish caught alive by Osprey. Many of these were salmonids, known for better escape capabilities because of their upward visual

orientation (Swenson 1979). Bald Eagles were opportunistic in their piracy of Ospreys; eagle pairs nesting near more Ospreys pirated most often.

Reservoir Management. Fish introductions, bass fishing and tournaments, and annual stocking of salmonids were readily exploited by Bald Eagles at Shasta Reservoir. However, eagles relying primarily on the presence of carrion may periodically experience food shortages in the short term if spawning and angling, the sources of most carrion, are affected by weather or reservoir levels. Prolonged, multi-year drawdown, a consequence of reservoir management at Shasta Reservoir during dry periods, may affect the standing crop of fish, anglers' boating habits, fish spawning habitats, and water temperatures, which may further affect the timing of spawning and distribution of fish. Single season drawdown, if occurring during spawning, may dewater centrarchid nests, although spotted bass tend to place their nests in fairly deep water, and are thus less susceptible (Sammons et al. 1999).

The positive relationship between mean spring reservoir pool elevations and Bald Eagle productivity at Shasta Reservoir suggests that lower reservoir levels may negatively affect productivity in Bald Eagles, possibly by reduction of prey availability. Bald Eagle productivity during our study period was at or above average (U.S. Forest Service unpubl. data), possibly as a result of higher water levels that followed this prolonged drought.

Decreases in reservoir volumes, nutrient input, and littoral spawning habitats associated with prolonged drawdowns reduce the bottom up flow of energy in the system, decreasing numbers of small prey fish, and then predatory fish (Ruzycki et al. 2001), such as bass. However, prolonged drawdowns (3–4 yr) control noxious aquatic vegetation, aerate and solidify bottom muds, and oxidize organic and mineral materials, releasing nutrients and other food sources upon reflooding (Keith 1975). Elsewhere, managers often purposely recreate these conditions by periodic drawdowns and subsequent refilling of reservoirs, when fish show rapid growth and increased numbers upon inundation (Miranda and Durocher 1986).

The annual lowering of reservoir levels in summer, typical at Shasta Reservoir even during wet years, improved foraging opportunities for Bald Eagles. In a way that was somewhat analogous to eagles exploiting fluctuating tides in estuaries and other marine environments (Watson et al. 1991, Elliott et al. 2005), eagles at Shasta Reservoir preyed on bass and

catfish when their feeding areas and nests were exposed in shallow water as lake levels dropped. Additionally, during a brief, extreme drawdown at Shasta Reservoir in the 1970s, P. Detrich (pers. comm.) observed that fish making spawning runs into tributaries were more accessible to eagles when they crossed shallow deltas upstream of the reservoir pool.

Despite the immediate benefits of lower reservoir levels that concentrate and expose live fish for eagles during a seasonal drawdown, the long-term effect of less lacustrine and littoral habitat availability (i.e., a smaller reservoir) during an extended drawdown is a reduction of both the standing crop of fish (Palter 1997) and Bald Eagle habitat (e.g., shallow coves disappear), which may increase competition between neighboring pairs. Reservoir levels at Shasta Reservoir are often low the entire year during dry years because they are managed each winter for flood control. Because irrigation and flood control take priority in the management of Shasta Reservoir, prey and habitat availability for Bald Eagles temporarily and perhaps unavoidably diminish during those periods.

Management Recommendations. As there are both positive and negative consequences for Bald Eagles from single-season and long-term reservoir drawdowns, it is difficult to recommend a departure from the current operations of Shasta Reservoir that would ultimately benefit Bald Eagles. A reservoir held at or near full capacity would probably support more pairs with less competition, provided that fish stocks did not diminish as a result of nutrient deficit. In the interest of optimizing eagle productivity as well as irrigation needs, minimum pool level requirements for managers could be based on prior relationships between productivity and reservoir levels. In the case of the regression model for Shasta Reservoir presented herein, average productivity for Shasta Reservoir (0.8 young/occupied territory) corresponded with an elevation of 312 m ASL, or a 13 m drop from full pool.

We believe the needs of eagles should be considered if any future introductions of fish species are planned; however, the continued stocking of salmonids is an apparent benefit, as it is elsewhere in California (Jackman et al. 1999). Because of high levels of recreational use on Shasta Reservoir, areas around shoreline nest sites are often closed to boaters during the breeding season. Although we saw some evidence that fish were more easily approached by our research boat and eagles sometimes hunted live fish in these closure areas, we believe that a similar approach of closing eagle for-

aging areas might be counterproductive, because anglers are an important source of carrion during the later breeding season.

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