1990 INTERIM REPORT

THE EFFECTS OF FLUCTUATING FLOWS FROM GLEN CANYON DAM ON BALD EAGLES AND RAINBOW TROUT AT NANKOWEAP CREEK ALONG THE COLORADO RIVER, ARIZONA

by

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NOTICE

This is an interim report with preliminary findings that are subject to change. The results of this study could change substantially prior to the completion of the final report, and any citation of this work before that time would be premature. All findings regarding fluctuating flows, in particular, may change dramatically because flow values provided to this study were inaccurate, and overestimated true flows. The results of the energetic simulation model may also change after site-specific variables are obtained from the study area. This study may not be cited in the literature or quoted without written permission from the authors.

EXECUTIVE SUMMARY

The ecology of bald eagles (Haliaeetus leucocephalus) and rainbow trout (Oncorhynchus mykiss) at and near the confluence of Nankoweap Creek along the Colorado River in Grand Canyon was studied in February and March 1990. The purpose of this study was to determine if fluctuating flows from Glen Canyon Dam influenced eagle foraging behavior and food consumption, particularly in relation to the abundance and movements of their prey base of spawning rainbow trout.

The winter concentration of bald eagles at Nankoweap Creek represents the largest and most regularly-occurring eagle concentration in the southwestern United States. Two to 26 wintering and migrating bald eagles were present in the study area on a daily basis throughout the study period. The peak of the eagle concentration occurred from February 11 to March 7 (25 consecutive days) when at least nine eagles were present daily. Twenty-six eagles were present at the height of the concentration on February 26.

Eagle abundance generally increased with increasing rainbow trout abundance in Nankoweap Creek. From February 25 to March 5, trout in Nankoweap Creek numbered over 1000 individuals in the 600 meter study reach. The peak of abundance occurred on March 2, when 1565 trout were counted. All trout observed during this time were either in spawning or post-spawning condition. This increased abundance of spawning trout in Nankoweap Creek corresponded with increased stream temperatures. Movements of

trout into Nankoweap Creek showed no correlation with releases from Glen Canyon Dam under the limited range of flows observed. Numbers of river tagged rainbow trout recaptured in Nankoweap Creek showed a significant correlation with discharges from Glen Canyon Dam. Above most intermediate and high flows, a greater number of river-tagged fish were recaptured in the creek. Trout were able to enter Nankoweap Creek at all flows observed during the study period.

A total of 890 eagle foraging events were documented during the study period. Most foraging events took place in Nankoweap Creek (78%), with fewer foraging events on shore (for carrion trout; 9%), in the river (8%), and in isolated riverside pools left by fluctuating flows (5%). The area within a 50 m radius of the creek mouth was the most heavily-used foraging habitat for eagles.

A highly significant difference existed between geographic patterns of foraging events at high versus low flows, indicating that fluctuating flows influenced eagle foraging behavior. Adult eagles foraging on live trout in the creek exhibited the greatest foraging success (85%) when different age classes and locations were compared. Foraging success on live trout was highest in isolated pools created by fluctuating flows for all age classes combined. A total of 11.5% of all prey items consumed by eagles were obtained from isolated pools or on shore near the creek mouth where they had been stranded by fluctuating flows. Adults were generally more successful at foraging and more diverse in

their use of foraging habitat than younger eagles. Forages in the creek were more successful than river forages.

A bald eagle energetic simulation model indicated that the eagle population at Nankoweap was able to consume an average of 6% more kilocalories/eagle/day than required for energetic equilibrium. Without the additional prey items provided by fluctuating flows, the eagle population would have consumed 5% fewer kilocalories/eagle/day than required for energetic equilibrium.

1990 PROJECT PERSONNEL

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INTRODUCTION

The operation of Glen Canyon Dam has recently created conditions for attracting both migrant and wintering bald eagles (Haliaeetus leucocephalus) to the Colorado River in Grand Canyon. Bald eagles were extremely rare visitors to the river corridor prior to construction of the dam and through the late 1970s (Brown et al 1989b). Small numbers of migrant and wintering eagles began frequenting the river at and near Nankoweap Creek in the early 1980s in response to the abundance of spawning rainbow trout (Oncorhynchus mykiss) there during fall and winter months. The numbers of eagles present at and near Nankoweap continued to increase each year until, by the winter of 1988, at least 18 eagles were present at the mouth of the creek and an unknown number occurred along the river in Marble Canyon upstream of the Little Colorado River (Brown et al. 1989b).

The winter concentration of bald eagles at the mouth of Nankoweap Creek has been made possible by a winter spawning run of rainbow trout. Trout were introduced into selected tributaries within the Park (not including Nankoweap) in the 1920s (Maddux et al. 1987). The completion of Glen Canyon Dam in 1963 lowered water temperatures and reduced turbidity in the Colorado River, creating the potential for a cold-water fishery. Trout then colonized the mainstream river, both from tributaries where they were already established and from introductions made at Lees Ferry. Trout inhabiting the river eventually found

winter conditions in Nankoweap Creek conducive to spawning, and a limited spawn was documented there in the winter of 1977-1978 (Carothers and Minckley 1981). The trout spawn has increased in size in the last decade (Maddux et al. 1987).

The trout spawn and, in turn, the eagle concentration at Nankoweap Creek may be influenced by fluctuating flows from Glen Canyon Dam. Influences to the eagle concentration would be manifested through fluctuations in their prey base, or by the dam's potential influence on their foraging behavior. The purpose of this study was to document any influence of fluctuating flows on spawning trout and migrant or wintering bald eagles. The null hypothesis was that fluctuating flows have no influence on the trout movement or the eagle concentration.

The objectives of this study were as follows:

1. Test the null hypothesis that eagle foraging patterns are not influenced by fluctuating flows.
2. Determine if eagle caloric intake is influenced by fluctuating flows.
3. Determine if eagle abundance is related to the abundance of spawning trout.
4. Document eagle foraging ecology, time and energy budgets, and the abundance and timing of the eagle concentration.
5. Determine trout abundance and describe spawning phenology in Nankoweap Creek.

6. Test the null hypothesis that fluctuating flows do not influence movement or abundance of spawning trout into the creek.

8. Determine the residence time of trout in the creek.

STUDY AREA

Nankoweap Creek is a small tributary entering the Colorado River from river right (as one faces downstream; the north bank) at River Mile 52, 110 km (67 miles) downstream from Glen Canyon Dam (Stevens 1983). The drainage basin comprises 84.4 km^2 on and below the Kaibab Plateau (Webb et al. 1987) at elevations between 880 and 2,900 m (2,750 and 9,000 feet). The creek flows 14 km (8.5 miles) to its confluence with the river; the elevation of the confluence is approximately 880 m (2,750 feet).

The creek is fed by perennial springs as well as runoff and winter/spring snowmelt from the Kaibab Plateau. Annual flows range from 0 to ca. 35 cfs (cubic feet/second), but winter flows normally range from 1 to 6 cfs (Johnson and Sanderson 1968). The lower 3.2 km of the creek exhibit clear, shallow riffle habitat, interspersed by pools with a narrow channel width at a typical winter flow of 1 cfs.

Nankoweap Creek enters the Colorado River through a broad delta (2 km across) which constitutes the widest portion of the Marble Canyon region of Grand Canyon above the Little Colorado River. The lowermost 500 m of the creek meander across the flat

Nankoweap delta and, with the surrounding canyon walls, provide ideal conditions for eagle foraging, soaring, and perching.

Typical winter release patterns from Glen Canyon Dam exhibiting strongly fluctuating flows were seen during the study period (Fig. 1). Flows released from the dam ranged from as low as 1,200 cfs to as high as 24,900 cfs.

The study area is lightly used for recreational activities (rafting and hiking) in February and moderately used in March. Twenty of the 43 total days of the study period were marked by recreational activities at or within 500 m of the mouth of Nankoweap Creek. Fourteen raft trips passed through the study area during the study period: 10 private or commercial trips, three research trips (all to support this study), and one National Park Service patrol trip. Five hiking parties also came down the Nankoweap or Saddle Mountain trails and visited the mouth of the creek.

METHODS

Avian Ecology

All information on eagle abundance and ecology was gathered through direct observation techniques from February 7 to March 20, 1990. No observations were made on February 19 due to snowfall. An observation post was established under an overhang on the high ridge downstream of the creek and ca. 700 m west of the creek mouth and 120 m above it. This observation post was manned continuously during daylight hours (30 minutes before

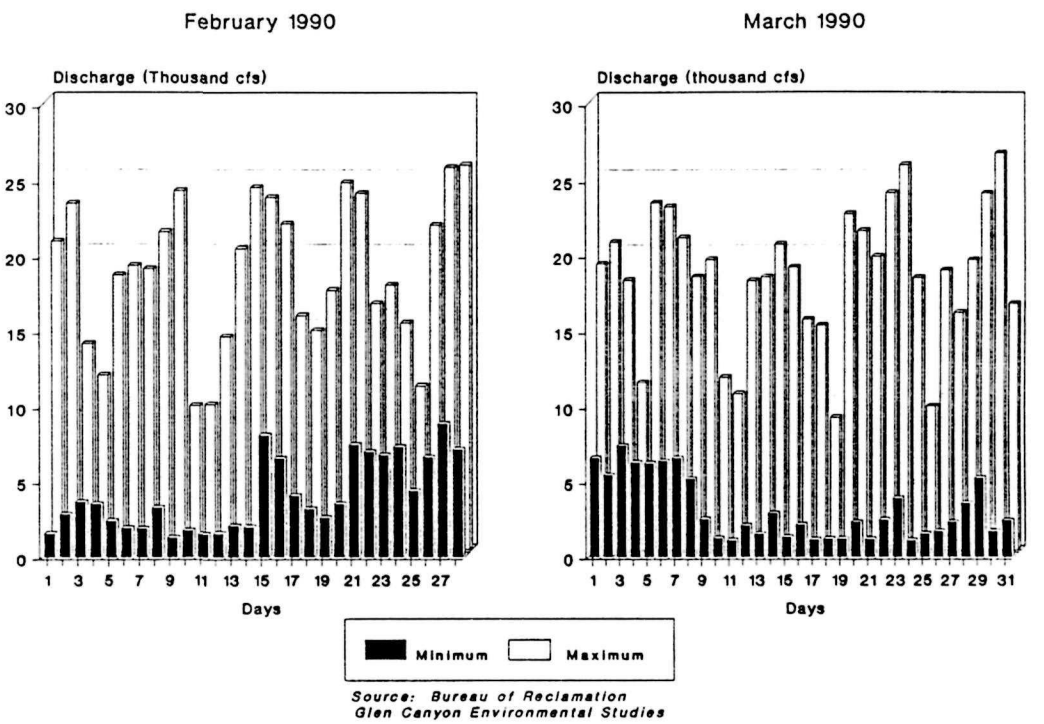


Figure 1. Maximum and minimum flows released from Glen Canyon Dam during February and March 1990.

sunrise and 30 minutes after sunset) by two to five observers equipped with binoculars and spotting scopes of up to 45 power. Observation crews were rotated at noon. From the observation post, observers had an unobstructed view that extended 5 km (3 miles) downriver and 2.5 km (1.5 miles) upriver.

All eagles coming into the study area were counted, with special emphasis on identifying different age classes and plumage patterns (Southern 1964, 1967; Bortolotti 1984; Clark 1987). The minimum number of eagles present in the study area per day was determined by adding the maximum number of individuals of each age class or plumage pattern seen at one time. Age classes that were easily recognizable were: adult, near-adult, osprey plumage (transition plumage), subadult (including whitebelly I and II), and immature. For the purposes of this report, adults included full adults and near-adults; subadults included osprey-plumaged (transition) individuals and whitebelly individuals; and immatures included all-dark first-year individuals.

Individuals occasionally exhibited unique plumage characteristics (missing feathers, unusual plumage patterns, leg bands, etc.) that would allow them to be counted over and above the daily total for those individuals exhibiting normal plumage patterns. If there was no reason, based on timing, plumage, or individual markings, that two separate observations of eagles were of different individuals, then those observations were considered to be the same individual. This conservative

assumption curbed the tendency to overestimate daily population size in the study area.

All eagle foraging events in the study area were recorded. Information gathered on each foraging event included: date, time, number of attempts, age class of eagle, success (yes or no), location, distance to nearest shore, prey status (alive, dead, unknown), prey type (trout or other), prey disposition (consumed or not), incidence of kleptoparasitism (piracy), and turbidity of attack site. A foraging event was defined as any attempt to secure prey, whether successful or not. A successful foraging event occurred when an eagle secured a prey item and began to consume it; prey that was pirated by a second eagle before the first eagle was able to begin eating was classified as a successful foraging event for the first eagle.

Activity patterns were quantified by visually following individuals and recording their activity by minute until they were lost from view (Craig et al. 1988), a method that provides the most reliable time budget estimates for birds that can be observed for long, uninterrupted periods (Bradley 1985). An important assumption of this technique was that the proportion of time/activity was the same when eagles were out of sight as when they were in sight. The five energetically-derived activities that were recorded were after those used by Stalmaster and Gessaman (1984): (1) perching, daytime standing on cliffs, boulders, on the ground, or in trees; (2) active flight (flapping); (3) passive flight (soaring); (4) feeding; and (5)

waiting to feed, standing near other feeding birds. Based on observations at roosts (night perches), 30 minutes after sunset to 30 minutes before sunrise was used as the average time spent roosting by all age classes. Time and activity budgets were calculated based only on those days (n = 12) of continual dawn-to-dusk observation when human disturbance at or near the mouth of the creek had not modified eagle behavior patterns.

An energetic simulation model was used to determine the energy budget of eagles present in the study area. The model was composed of two submodels: (1) the daily energy intake submodel which estimated the eagles' daily caloric intake (as determined by the mean number of fish consumed/eagle/day); and (2) the daily energy expenditure submodel which estimated the eagles' daily caloric expenditure (based on weather, temperature, and activity costs). This model (Fig. 2) is a modified version of that described in detail by Stalmaster (1981a, 1981b, 1983) and Stalmaster and Gessaman (1984).

The daily energy intake (DEI) submodel required data on the number of eagles present/day (A), the total number of trout consumed by the eagle population/day (B), the average weight of trout (C) after being multiplied by the amount of the carcass that is edible, the average proportion of a trout that was consumed after competition or other loss (D), and the average number of kilocalories (kcal)/gram of trout (E) adjusted for prey status (alive [E_a], carrion [E_c], or unknown [E_u]). The resulting

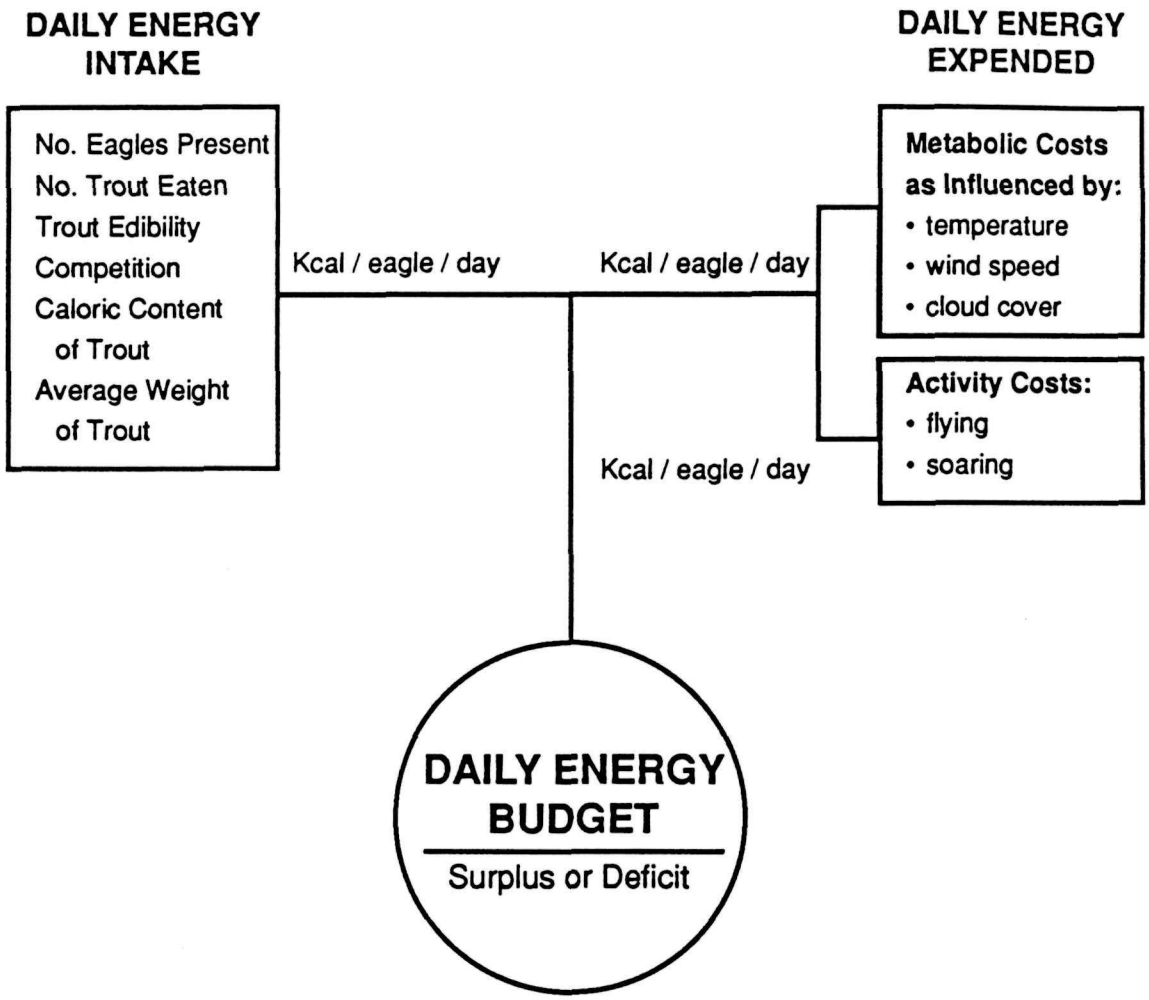


Figure 2. Components of the bald eagle energetic simulation model.

calculations for DEI were:

$$DEI = ([B \times C \times D] \times E)/A = \text{kcal/eagle/day}.$$

Average trout weight was determined to be 539 g, as determined from both unpublished data gathered by the Arizona Game and Fish Department and data gathered during this study. The average weight of trout was multiplied by its edibility quotient, determined by Stalmaster (1983) for coho salmon (Oncorhynchus kisutch) as 78.7%. The average loss to competition from common ravens (Corvus corax), golden eagles (Aquila chrysaetos), and other factors (including abandonment and loss of prey) was estimated at 6% (Stalmaster 1983). The average weight of trout (after being adjusted for its edibility) was multiplied by 0.94 to account for this loss. Wet-matter energy of rainbow trout prior to decomposition was assumed to be 0.90 kcal/g (after the number of kcal/g of coho salmon given in Stalmaster 1983). Decomposition of carrion trout reduced biomass quantity as well as energy content, resulting in daily food energy declines of ca. 1.1%/day (after Stalmaster 1981b); therefore, all carrion consumed from on land or in water was reduced in caloric content to 0.8901 kcal/g, estimating an average duration as carrion of one day. Trout of unknown status (not known if taken alive or as carrion) were calculated to have an energy content intermediate to live and carrion trout, and were reduced in caloric content by a value of 0.55%/day, to 0.89505 kcal/g.

The daily energy expenditure (DEE) submodel required data on mean daily temperature, wind speed, cloud cover, and the

proportion of the 24-hour day spent in active (flapping) flight and passive (soaring) flight. The DEE submodel is almost identical to the daily energy consumption submodel of Stalmaster (1983), with the exception that our DEE submodel does not partition the day into Stalmaster's three habitat subcomponents (feeding, perching, and roosting). The DEE submodel of this study assumes that ambient climatic conditions in those three habitats did not differ. The DEE submodel was computed by:

$$\text{DEE (kcal/eagle/day)} =$$

$$D[GEI + (M_{day} - SMR_{day})] + N[(GEI + (M_{night} - SMR_{night})]$$

$$+ [\text{Flap} \times \text{BMR}] + [\text{Soar} \times \text{BMR}]$$

where D and N are percent of daytime and nighttime coefficients, and flap and soar represent the mean amount of time spent in those two activities. Calculations for gross energy intake (GEI) were after Stalmaster (1983); metabolic heat production (M) and standard metabolic rate (SMR) are provided in detail by Stalmaster (1981a, 1981b, 1983). Basal metabolic rate (BMR) is a constant of 2.77 cal/g/hour; flapping costs are 12.5 x BMR, while soaring costs are 3.5 x BMR (see Stalmaster 1981b, 1983). The National Oceanic and Atmospheric Administration provided climatic data. Ambient daily temperatures were from Phantom Ranch (ca. 50 km downriver from Nankoweap Creek); mean daily wind speed and cloud cover were from the Tusayan airport on the South Rim.

The average daily energy budget of a bald eagle in the study area is expressed by: DEI - DEE = kcal/eagle/day. If the resulting figure is positive, then eagles are consuming more kcal

than they are expending, for a net energy surplus; if negative, then the eagles are expending more kcal than they are consuming, for a net energy deficit. The null hypothesis was that the eagles maintained a balanced (DEI - DEE = 0) energy budget.

A logistic regression model (Cox 1970) was used to test the null hypothesis that increasing river flow levels would not affect the location of foraging events in the creek. All flow values were transformed to a more manageable magnitude by dividing by a scale factor of 10,000. Foraging events within 50 m of the creek mouth (n = 559) were treated as a discrete event, as were foraging events greater than 75 m upcreek of the mouth (n = 139) since no foraging events occurred between 50 m and 75 m upcreek. Only one group of upcreek data was desirable in order to counterbalance the large proportion of data within 50 m of the mouth. The computations were made using the NONLIN module of SYSTAT (Version 4; Wilkinson 1989).

Aquatic Ecology

Physio-chemical Analysis

A Hydrolab Datasonde DS2H (Series 2270) was installed in Nankoweap Creek to record water temperature, dissolved oxygen, pH, and conductivity continuously over the study period. In addition, a Yellow Springs Instruments dissolved oxygen and

temperature meter (Model 51B) was used to record data during each fish sampling period.

Stream discharge from Nankoweap Creek was measured in the lower 100 meters of the creek periodically throughout the study. A Marsh-McBirney current meter mounted on a standard wading rod was used to measure stream velocity. Stream width and depths were taken at each cross-section. Cross-sections to determine discharge were replicated at each sample site.

Stream morphology of Nankoweap Creek was described by percent substrate in each reach (described below under Trout Abundance), pool size, and channel depth. Substrate was analyzed by visually assessing random points, generated by a random number chart, along the stream. The general substrates consisted of silt, sand, gravel, cobble, boulder and vegetation. Substrate was classified as armored where stream bottom was highly compacted and cemented.

Trout Abundance and Spawning Phenology in Nankoweap Creek

Rainbow trout abundance in Nankoweap Creek was determined by visually counting individual fish. All fish collected were visually classified by reproductive condition (spawning coloration and/or presence of eggs and milt), measured, tagged and released. Reproductive condition of trout was classified as either non-spawning, pre-spawning, actively spawning or post-spawning (spent). Pre-spawning trout had bright coloration in males and eggs were present in females, but not

ready to be released. Spawning trout had eggs and milt easily emitting from the fish. Spent trout showed obvious loss of eggs in females with sagging abdomens and poor body condition in males (worn fins, loss of scales, etc.) The proportion of spawning to non-spawning fish was used to indicate the height of spawning activity, as well as changes in spawning activity over the study period.

The number of trout in Nankoweap Creek was counted during various river flows. Abundance was determined primarily at night to minimize impacts on bald eagle behavior. Night counts were also more accurate than day counts because fish were less excitable after dark.

Nankoweap Creek was divided into three 200 m reaches, beginning at the mouth and extending 600 m upcreek. Reach 1 was 100-200 m, Reach 2 was 200-400 m, and Reach 3 was 400-600 m from the mouth. Sampling was conducted at least three nights per week during the eagle census period. Standard (SL) and total length (TL) were measured to the nearest millimeter (mm). Sex and reproductive condition were determined non-destructively for all fish sampled. Trout abundance was recorded for each study reach, then combined for a total count. Counts of fish were very accurate in the run and riffle habitats and pools when abundance was low. With increased numbers, trout densities in pools had to be estimated by taking the average of 3-4 counts by several workers. Rainbow trout were extremely rare above 600 m, therefore our study area ended at the end of Reach 3.

Trout Movement

At the beginning of the study period, a sample of rainbow trout was obtained from the river by angling. These trout were marked with individually numbered Floy tags, measured, and reproductive condition visually determined. During this capture effort the creek mouth was blocked to assure that a known number of marked fish were added to the river population.

The movement of rainbow trout into Nankoweap Creek was observed under various flow regimes from Glen Canyon Dam. Direct observations were conducted at night and during the day throughout the study. In addition, the number of river tagged fish recaptured in Nankoweap Creek under varying flows was used.

Trout movements (fish per hour) into Nankoweap creek were counted at the creek mouth 3-4 nights per week. Additional daytime counts were conducted from the observation post using spotting scopes. The shallow depth of the mouth of Nankoweap Creek afforded clear visibility to count incoming trout. These movement data were compared with river discharges to determine if flows influence movement into the creek.

Data used in correlating trout movements with temperature and river discharge are based on times when trout were motivated by spawning behavior to enter Nankoweap Creek. The period of February 16 to March 2, when fish were assumed to be motivated by spawning activities, was used. After March 2, the peak of abundance, motivation to spawn was assumed to be waning.

During the early part of this study, a weir was set-up near the mouth of Nankoweap Creek to trap incoming fish. This weir was used until the total number of fish in the creek reached 700 individuals. At this time the weir was abandoned because of potential adverse impact on fish spawning behavior.

Direct observations were initiated after abandonment of the weir to determine trout movement into Nankoweap Creek under various river discharges. Because of fluctuating river levels, the actual creek mouth "moved" with changing flows. Fish were considered "entered" when they reached the shallow riffle above "Gordo's" rock (a prominent boulder above most river flows observed) or had travelled 15 m above the river level at the time of observation.

Trout Residence Time in Nankoweap Creek

A minimum of 50 fish in each reach were marked with individually numbered Floy tags: pink for Reach 1, yellow for Reach 2 and red or orange for Reach 3. Rainbow trout tagged in the Colorado River were tagged with green Floy tags to distinguish them from creek fish. As fish moved into and out of Nankoweap Creek new fish were tagged to keep a large number of tagged fish in the creek.

Residence time per fish per reach was determined by adding the number of days each fish spent in each reach. It was assumed that the first day a fish was tagged counted as one full day.

The last day a fish was recaptured was also considered a full day of residence time.

Analysis and Presentation of Flow Data

Colorado River discharge at Nankoweap Creek was estimated by subtracting two hours from measured discharges at the U.S. Geological Survey (USGS) gaging station above the mouth of the Little Colorado River (15 km, or 9 miles, downstream of Nankoweap). Two hours were subtracted to allow for an average of approximately two hours lag time for water to move from Nankoweap to the Little Colorado River. The Little Colorado gage was the closest gaging station to the study area, and thus provided the best possible measure of the magnitude and timing of maximum and minimum flows moving past Nankoweap Creek.

Provisional flow data provided by the USGS from the Little Colorado River gage were inaccurate. Discharges for the Little Colorado River gage during the study period ranged from lows of ca. 6,400 cfs to highs of ca. 31,500 cfs. Actual low releases reported from Glen Canyon Dam were approximately 5,000-6,000 cfs less than the Little Colorado flow values, and our personal observations suggested that river flows at Nankoweap may have gone as low as 2,000 cfs. Maximum high releases from the dam were approximately 6,500 cfs less than the Little Colorado flows, and maximal flows at Nankoweap probably never equalled those releases from the dam due to attenuation as the release moved

downstream. Overall, flow data from the Little Colorado gage appeared to overestimate actual flows by 5,000 to 7,000 cfs.

Despite problems with accurate estimation of flows, data from the Little Colorado gage were used in the eagle foraging and trout movement analyses. We felt the Little Colorado gaging data portrayed the hour-by-hour relative change (not absolute change) in river flow for the study area better than the alternative of manually calculating flows downstream from either the dam or Lees Ferry. Since the absolute values of the flows from the Little Colorado gage were proportional (by some unknown factor) to the true flows, we presented the data on a relative scale. Therefore, the only flow values presented or discussed in this report are for "low," "intermediate," and "high" flows. For the purposes of this interim report, low and high flows represent the lowest and the highest flows experienced in the study area during the study period. "Intermediate" flows lie between the highest and lowest flows experienced in the study area during the study period. The true values of these flows will probably not be known until 1991, when the USGS can recompute the Little Colorado gaging data.

RESULTS

Avian Ecology

Abundance and Timing of the Eagle Concentration

Two to 26 bald eagles were present in the study area on a daily basis throughout the study period. The peak of the eagle

concentration occurred from February 11 to March 7 (25 consecutive days) when at least nine eagles were present each day (Fig. 3). More than 20 eagles/day were present on five days during the period of February 26 to March 4.

The number of eagles/day gradually increased through February as the number of trout in the creek increased (Fig. 3). However, the number of eagles/day declined sharply in early March although trout abundance remained high.

Eagle Time and Activity Budget

Activities of bald eagles of all age classes were followed for 452.8 hours. The predominant daytime activity of eagles of all age classes was perching (Table 1). Adults spent the greatest proportion of time perched (the least energetic activity type); adults also spent the smallest proportion of time flapping (the most energetic activity type), the smallest proportion of time feeding, and the greatest proportion of time waiting to feed. In contrast, immatures spent the greatest proportion of time flapping and feeding, and the smallest proportion of time waiting to feed.

Foraging Ecology

A total of 890 foraging events were documented during the study period. Foraging took place throughout the day, with peaks of foraging activity from 0700 to 1000 hours and 1300 to 1600 hours (Figure 4). All attempted forages were for trout or for

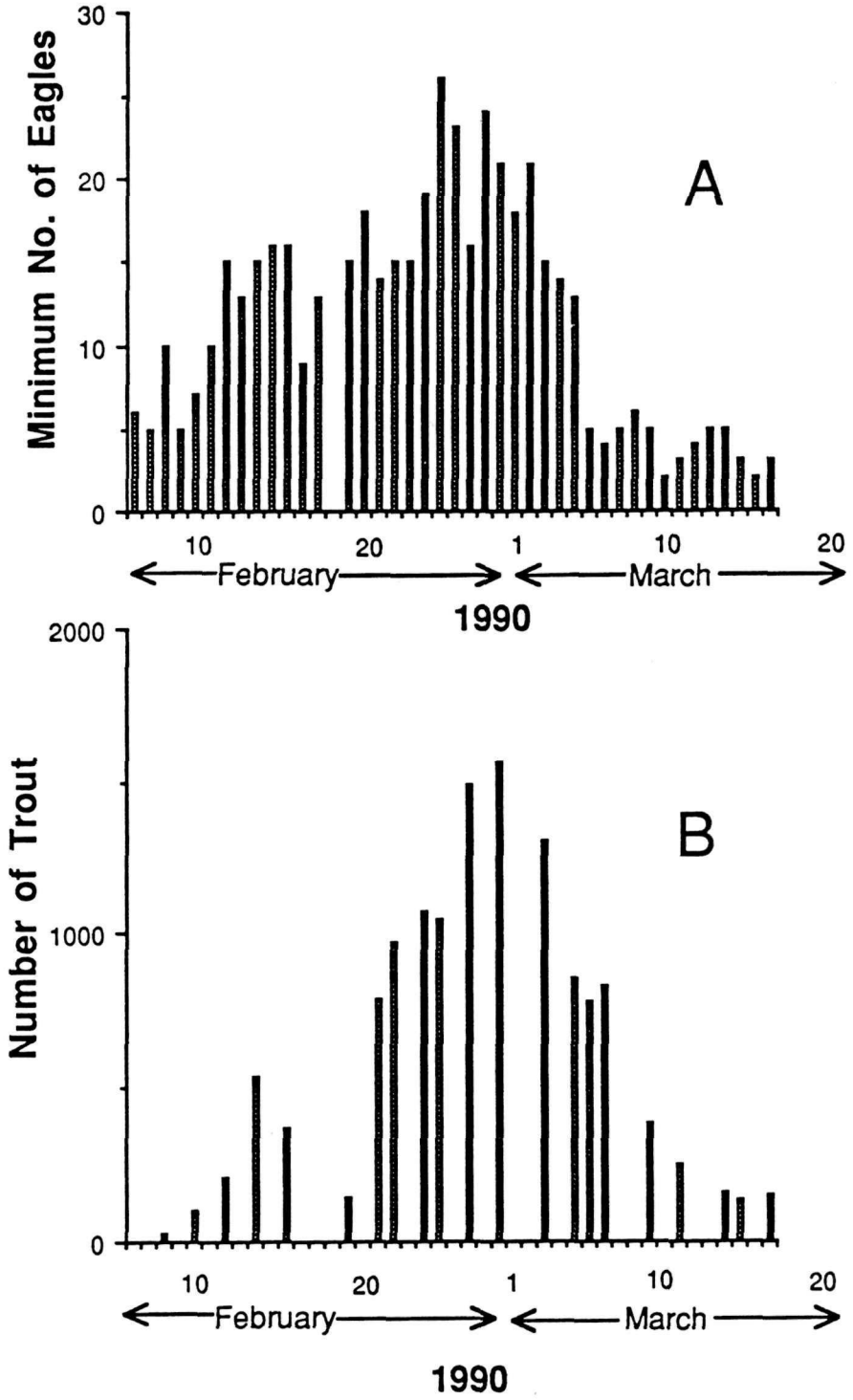


Figure 3. Minimum number of bald eagles/day at and near Nankoweap Creek (A) and number of rainbow trout/day in Nankoweap Creek (B) along the Colorado River, Grand Canyon, February and March 1990.

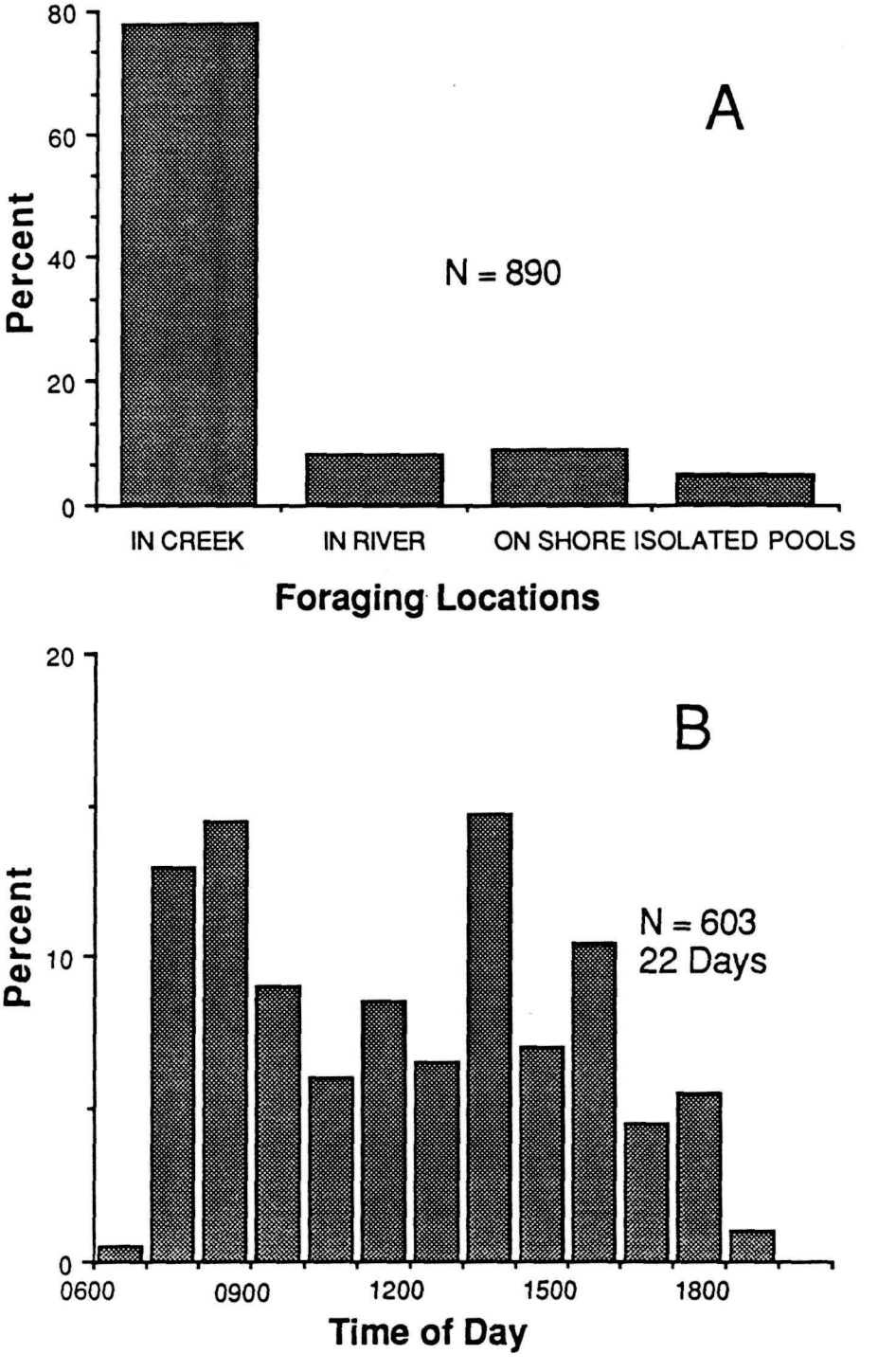


Figure 4. Percent of bald eagle foraging events by foraging location (A) and by time of day for 22 days without human disturbance (B), Nankoweap Creek, Colorado River, Grand Canyon, February and March 1990.

Table 1. Daytime activity budgets of bald eagles along the Colorado River at Nankoweap Creek, Grand Canyon, February to March 1990. Only full observation days without human disturbance were included (n = 12).

	Percent of Time			
Activity	Adults	Subadults	Immatures	All Age Classes
Perch	81.7	74.8	80.1	78.4
Active Flight	3.3	3.5	3.6	3.4
Passive Flight	4.4	10.0	3.4	6.8
Feed	6.1	8.6	12.1	8.1
Wait to Feed	4.5	3.1	0.8	3.3
Total	100.0%	100.0%	100.0%	100.0%
Total No. Observation Minutes	10,898	12,121	4,148	27,167

unknown fish assumed to be trout, except for one unsuccessful attempt on waterfowl in the river just downstream of the creek mouth.

Foraging events took place in four locations: in Nankoweap Creek, in the Colorado River within 200 m of the mouth of the creek, on shore along the banks of the creek or river (these were usually carrion trout), and in isolated pools left by fluctuating river flows. The majority of foraging activity occurred in the creek (78%; Fig. 4).

Seventy-eight percent of all bald eagle foraging events were recorded within 50 m of the confluence of the creek and the river. Eighty percent of all creek forages took place within 50 m of the mouth of the creek (Fig. 5), as did 83% of river forages (Fig. 5), 64% of forages on shore (Fig. 6), and 56% of forages in isolated pools (Fig. 7).

The proportion of foraging events in each of the four foraging locations varied by age class (Table 2). All age classes foraged primarily in the creek, but adults made proportionally smaller use of the creek and greater use of river, shore, and isolated pool foraging locations.

Overall eagle foraging success in the study area was 73%, but varied widely between age class and foraging location (Table 3). Adults exhibited the greatest success rate in all locations where an adequate sample size was obtained. Subadults and immatures had similar, but lower, foraging success. Foraging success was highest in isolated pools; foraging success was much higher in

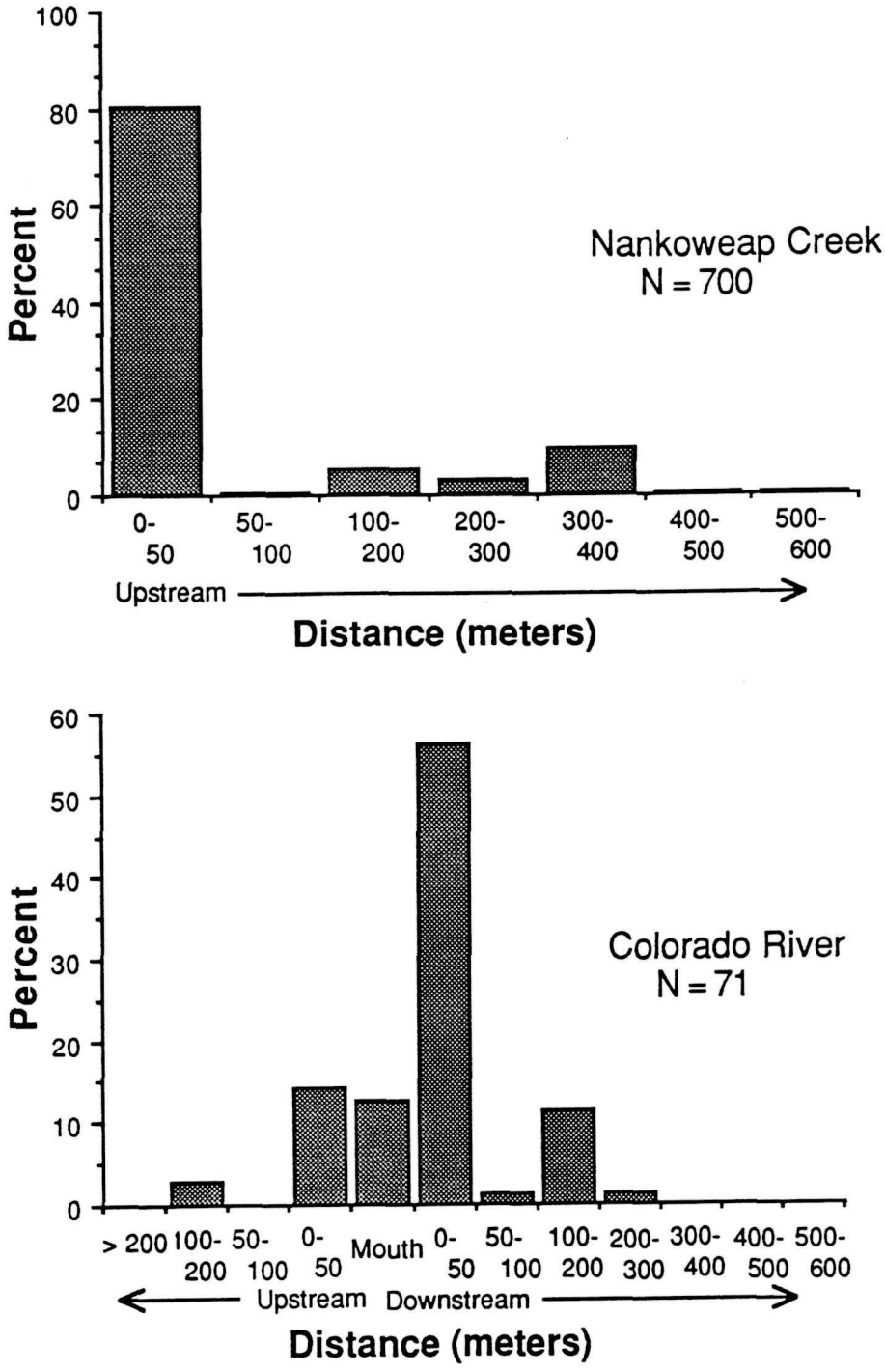


Figure 5. Location of bald eagle foraging events in Nankoweap Creek (top) and in the Colorado River within 600 m of the creek (bottom), Grand Canyon, February and March 1990.

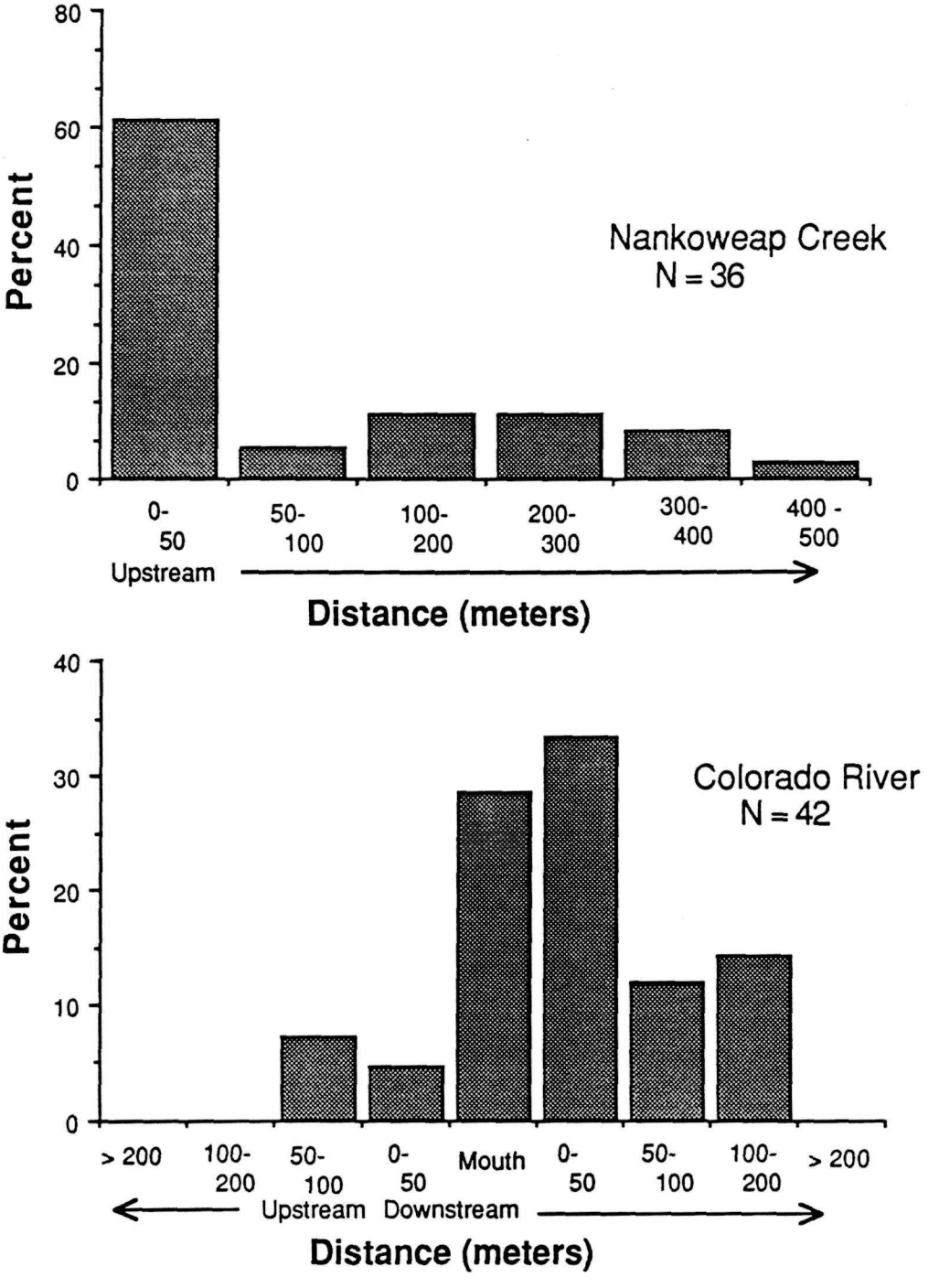


Figure 6. Location of bald eagle foraging events on shore along Nankoweap Creek (top) and on shore along the Colorado River within 600 m of the creek (bottom), Grand Canyon, February and March 1990.

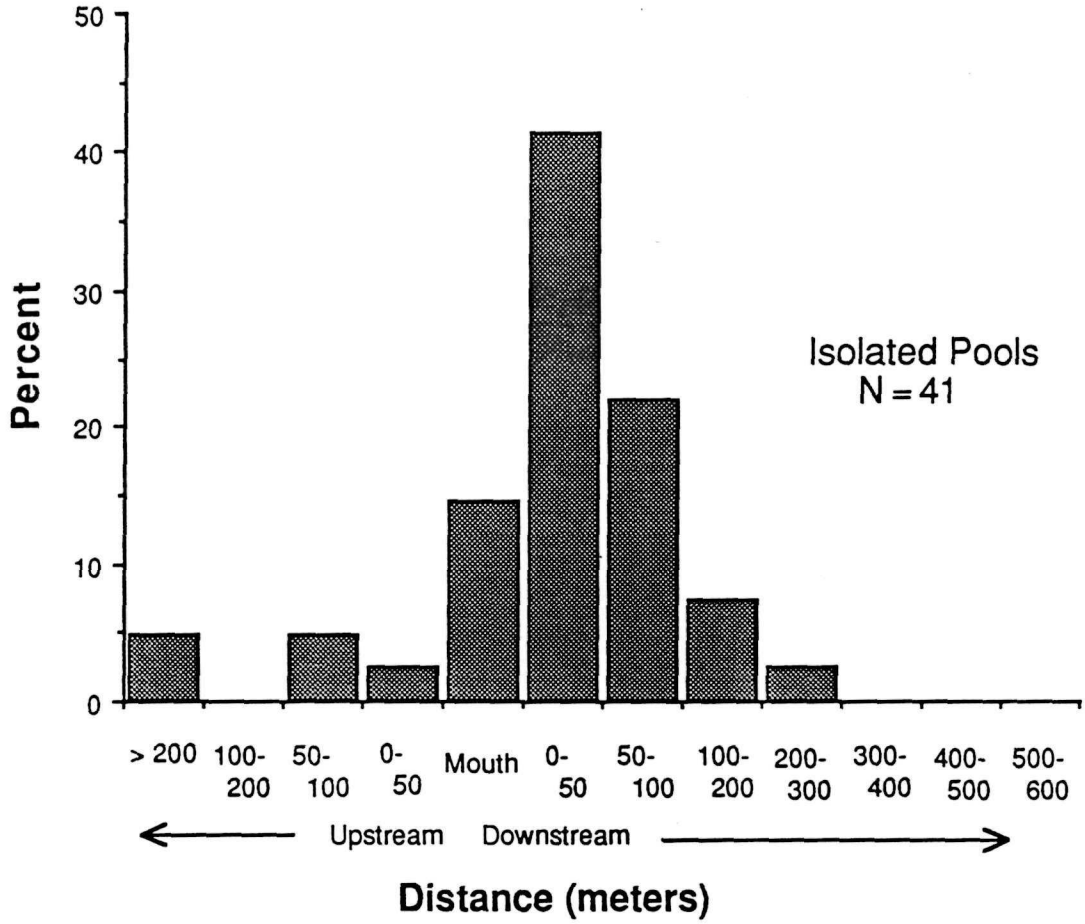


Figure 7. Location of bald eagle foraging events in isolated pools along the Colorado River within 600 m of Nankoweap Creek, Grand Canyon, February and March 1990.

Table 2. Percent of foraging events by location and age class for bald eagles at or near Nankoweap Creek along the Colorado River in Grand Canyon, February to March 1990. Successful and unsuccessful foraging events have been combined; n = sample size.

	Location									
	Nankoweap Creek		Colorado River		Shore		Isolated Pools		All	
Age Class	n	%	n	%	n	%	n	%	n	%
Adult	143	64	26	12	32	14	22	10	223	25
Subadult	423	83	36	7	34	8	14	2	507	57
Immature	130	83	9	6	12	7	5	2	156	18
All Age Classes*	696	78	71	8	78	9	41	5	886	100

* The total number of forages here (886) does not equal the total number of forages observed (890) because of missing age data for four foraging events in the creek.

Table 3. Bald Eagle foraging success by age class and location, at or near Nankoweap Creek along the Colorado River, Grand Canyon, February to March 1990. Only foraging events involving live fish have been included.

	Location							
	Nankoweap Creek		Colorado River		Isolated Pools		All Locations	
Age Class	n	% Success	n	% Success	n	% Success	n	% Success
Adult	133	85	20	65	6	83	159	82
Subadult	402	73	35	34	9	67	446	70
Immature	128	74	6	50	4	100	138	74
All Age Classes	663	76	61	46	19	79	743	73

the creek than in the river. Table 3 does not include data for forages on shore (usually carrion, sometimes pirated from common ravens) because they were all successful.

Foraging success on live trout also varied with location within the creek and within the river. Considering all age classes combined, foraging success was 73% in the lowermost 100 m of the creek and 78% for all forages between 100 and 600 m. The average distance upcreek of all forages in the creek was 48 m; the average distance upcreek of all successful forages was 50 m.

Foraging events in the river were more successful near shore than farther out in the current. The average distance to shore for all river forages was 2.2 m; however, the average distance to shore of a successful river forage was 1.7 m, while an unsuccessful river forage averaged 2.7 m from shore.

Bald eagles exhibited a generalized attack strategy on live trout in the majority of foraging events in both the creek and the river. A foraging eagle would perch on the shore or a streamside boulder (74% of creek forages, 96% of river forages) for a short time before hopping or jumping (62% of creek forages, 46% of river forages) an average distance of 3 m (n = 586) onto a trout. If the foraging event was successful, the eagle would either begin eating the trout at the foraging site or drag it to shore to consume (82% of creek and river forages combined).

Energetic Simulation Model

The energetic simulation model indicated that the eagle population exhibited a net energy surplus of 16,954.2 kcal during the study period. Overall, mean energy consumption/day (484.9 kcal/eagle/day; SD = 312.4) exceeded mean energy expenditure/day (455.2 kcal/eagle/day, SD = 5.6; Table 4). Bald eagles at Nankoweap Creek consumed an average of 29.7 kcal/eagle/day above metabolic requirements, or 6% above their mean energy expenditure.

Mean energy consumption on days without human disturbance was 531.9 kcal/eagle/day (SD = 208.5), while mean energy consumption on days with human disturbance was 430.6 kcal (SD = 400.5). Energy expenditure on non-disturbed days (456.0 kcal/eagle/day) was similar to disturbed days (454.1 kcal/eagle/day). Bald Eagles at and near the mouth of Nankoweap Creek were able to consume a surplus of 76.7 kcal/eagle/day on those days without human disturbance; on days with human disturbance, their food consumption resulted in a mean deficit of 23.5 kcal/eagle/day, or 5% below their mean energy expenditure.

Effect of Fluctuating Flows on Eagle Food Intake and Foraging Patterns

Of the 41 total foraging events that occurred in isolated pools (Table 2), 37 (19 live trout, 18 carrion trout) were successful. All of the 78 foraging events that took place on shore for carrion trout were successful; 42 of these occurred

Table 4. Mean daily energetic consumption and expenditure per eagle for Bald Eagles at and near the confluence of Nankoweap Creek and the Colorado River, Grand Canyon, February and March 1990.

Date	Mean Number Kcal Consumed Per Eagle	Mean Number Kcal Expended Per Eagle	Minimum Number Eagles/Day Present	Did Human Disturbance Occur?
2/07	142.0	458.2	5	Yes
2/08	287.1	459.0	10	No
2/09	569.4	457.3	5	No
2/10	766.2	456.2	7	No
2/11	714.0	455.4	10	No
2/12	477.2	457.6	15	No
2/13	441.0	448.0	13	No
2/14	669.8	459.4	15	No
2/15	290.8	468.4	16	No
2/16	536.9	467.6	16	Yes
2/17	39.4	467.5	9	Yes
2/18	589.0	461.5	14	No
2/20	806.8	458.6	16	No
2/21	418.3	456.1	18	Yes
2/22	614.9	454.0	14	Yes
2/23	537.8	453.3	16	Yes
2/24	380.3	454.4	16	No
2/25	528.6	452.9	19	No
2/26	703.6	455.5	26	No
2/27	62.4	453.0	23	Yes
2/28	627.2	450.2	16	Yes
3/01	462.9	451.8	24	Yes
3/02	836.1	453.9	21	No
3/03	418.0	451.7	18	No
3/04	785.3	452.8	21	No
3/05	597.6	455.9	15	No
3/06	102.3	456.4	14	Yes
3/07	110.4	449.9	13	Yes
3/08	71.0	454.5	5	Yes
3/09	178.4	448.9	4	No
3/10	71.8	449.1	5	Yes
3/11	238.6	453.8	6	No
3/12	639.6	462.7	5	Yes
3/13	532.4	463.5	2	No
3/14	0.0	456.4	3	Yes

Table 4. (continued)

Date	Mean Number Kcal Consumed Per Eagle	Mean Number Kcal Expended Per Eagle	Minimum Number Eagles/Day Present	Did Human Disturbance Occur?
3/15	177.5	452.9	4	No
3/16	713.0	455.2	5	No
3/17	714.6	452.4	5	Yes
3/18	955.0	445.3	3	Yes
3/19	1598.1	444.0	2	Yes
3/20	477.2	446.2	3	Yes
Mean	484.9	455.2		
SD	312.4	5.6		

immediately adjacent to the river. Therefore, 79 trout (37 plus 42; 19 live trout, 60 carrion trout) consumed by eagles were furnished by fluctuating flows, or 11.5% of all prey items consumed by eagles in the study area. This contribution to the eagles' total dietary intake represented 26,937.2 kcal (11% of all kcal consumed), after being adjusted for edibility, competition, and decomposition. Without the contribution of fluctuating flows, the overall eagle energy budget would have been 5% below the mean energy expenditure.

Flow values were assigned to 890 bald eagle foraging events at and near the mouth of Nankoweap Creek. The distribution of these foraging events by river flow level approximated a normal distribution (Fig. 8). A comparison of foraging events in or along Nankoweap Creek more than 100 m upcreek of the mouth versus all other foraging events (in the river, isolated pools, or in the creek within 100 m of the mouth) by flow indicates that flow-dependent geographic foraging patterns existed during the study period (Fig. 9).

At low river flows, no foraging events occurred more than 100 m up the creek; as flows increased, a greater proportion of foraging events occurred more than 100 m upcreek; at the highest flows experienced during the study period, approximately two-thirds (67%) of all foraging events took place more than 100 m upcreek.

Considering only those forages on live trout in the creek (78% of all foraging events; n = 698), the probability that a foraging

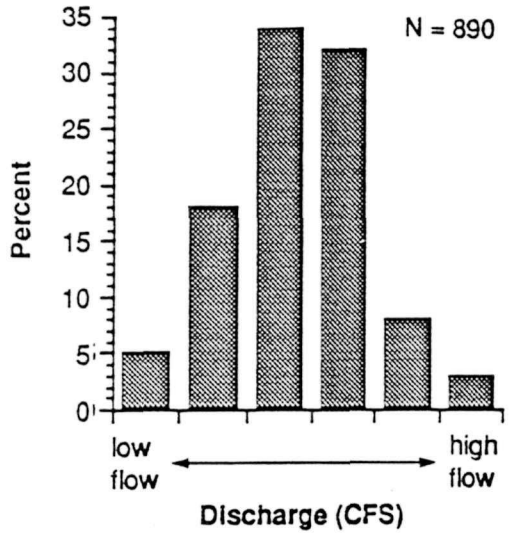


Figure 8. Percent of bald eagle foraging events that occurred at various flow levels, at and near the confluence of Nankoweap Creek with the Colorado River, Grand Canyon, February and March 1990. The six bars represent sequential 5,000-cfs flow categories arranged from the lowest to the highest flows.

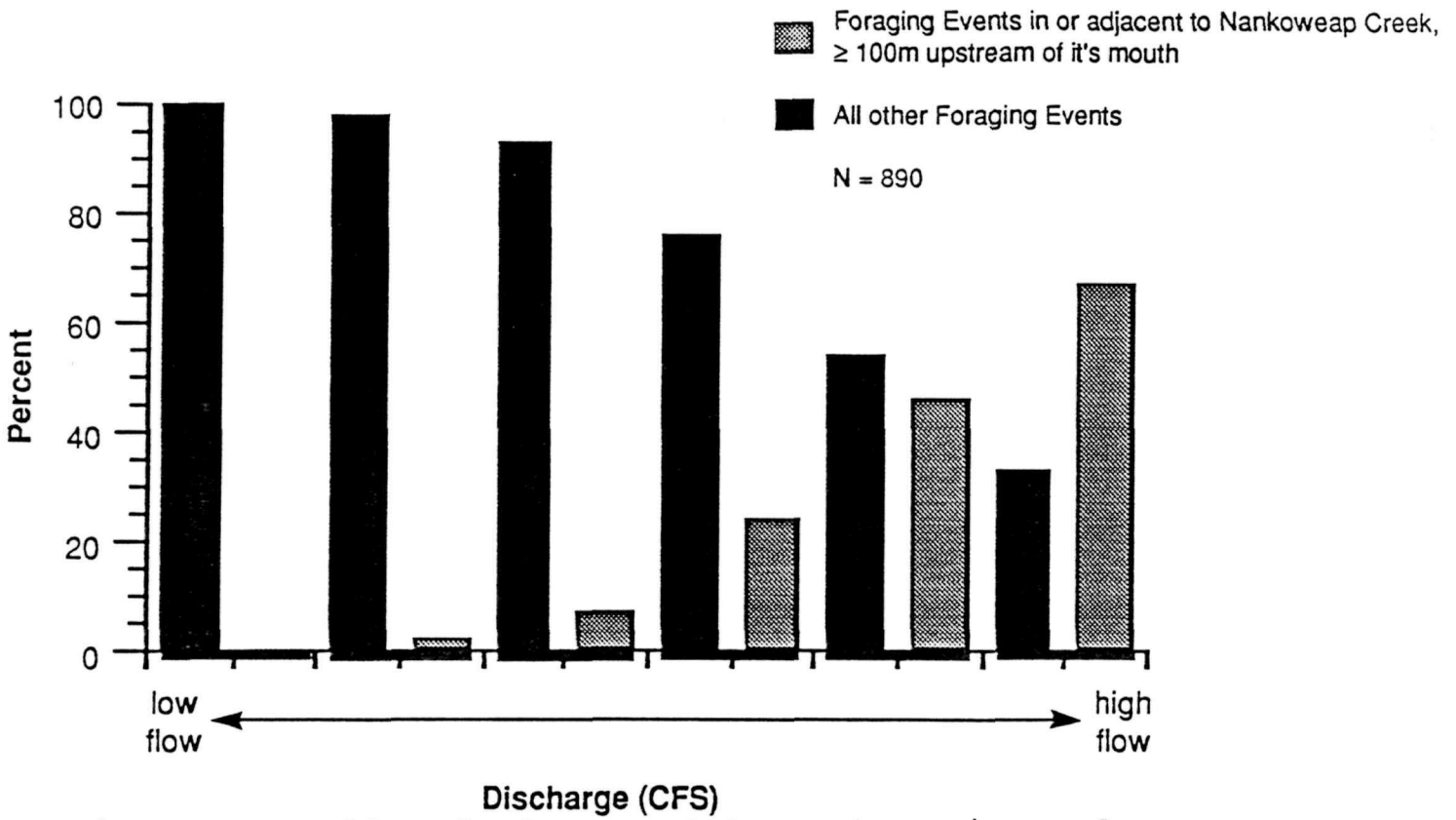


Figure 9. Bald eagle forages >100 m upstream in or along Nankoweap Creek versus other forages. Pairs of bars represent percentages of forages at 5,000-cfs flow categories from the lowest to the highest flows.

event would occur within 50 m of the creek mouth at the lowest river flows observed during the study period was 0.9951 and at the highest river flows seen during the study period was 0.1330 (Fig. 10). This flow-dependent change in foraging patterns was most pronounced at intermediate river flows. A very highly significant difference existed between the number of creek forages within 50 m of the creek mouth at high and low flows versus the number of forages greater than 75 m up the creek at high and low flows (logistic regression; $z = 10.27$; two-sided p-value of 1.5×10^{-23}).

The percent of all foraging events that took place in Nankoweap Creek increased with increasing flows (Fig. 11). At the highest flows observed during the study period, 97% of all foraging events were in the creek. Foraging events on shore (usually for carrion) were most frequent at the lowest flows observed during the study period, and were nonexistent at the highest flows. Foraging events in the river and in isolated pools decreased in frequency as flows increased.

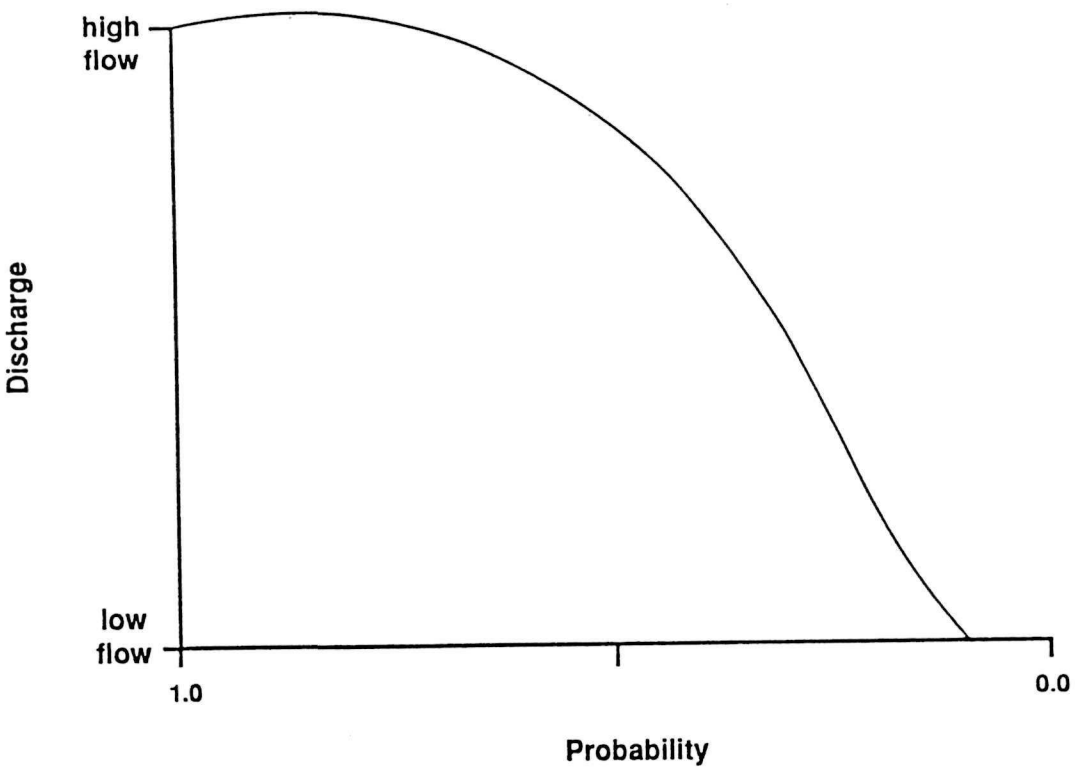


Figure 10. The probability, by river flow, that any given bald eagle foraging event for live trout in Nankoweap Creek was within 50 m of the confluence of the Colorado River, Grand Canyon, February and March 1990. River flow levels range from the lowest to the highest flows received during the study period.

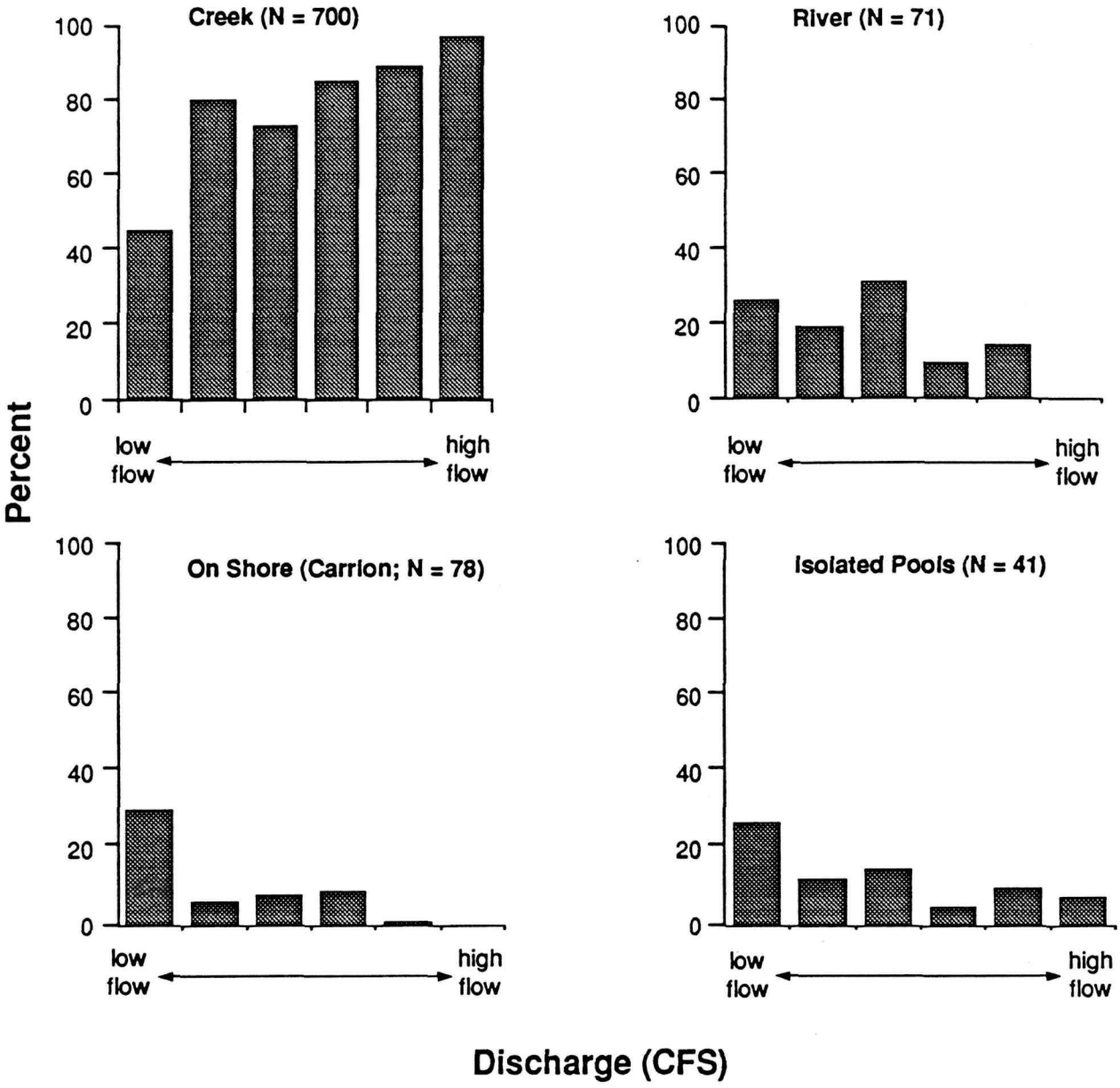


Figure 11. Percent of bald eagle foraging events by foraging location and river flow level, at and near the confluence of Nankoweap Creek on the Colorado River, Grand Canyon, February and March 1990. The six bars represent sequential 5,000-cfs flow categories arranged from the lowest to the highest flows received during the study period.

Aquatic Ecology

Physio-chemical Analysis

Water temperature in Nankoweap Creek was highly variable throughout the course of the study. Temperatures ranged from 0.14 to 17.9°C . Daily ranges frequently exceeded 10°C during February and March. This is typical of low volume, shallow streams (Hynes 1970). Stream temperatures in early February were below the preferred temperatures (10-12°C) for spawning rainbow trout (Scott and Crossman 1973), but rose rapidly by months end to well within preferred ranges.

Dissolved oxygen also varied during the study, consistent with the ability of cooler water to hold oxygen (Wetzel 1975). Although the dissolved oxygen concentrations varied widely, they never fell below the levels necessary for trout survival (Carlander 1969).

Conductivity and pH were relatively stable during the course of study. These parameters are available only for half of the field effort due to subsequent equipment failure.

Stream discharge in Nankoweap Creek averaged 0.86 cfs (n = 13, range = 0.54 - 1.14 cfs). The variability in estimated discharges is due to subsurface flow within the stream gravels (Dunne and Leopold 1978) and heterogeneity of the stream channel. No spates was observed during the study period.

Stream substrate was dominated by gravels in all three study reaches (Table 5). Gravel was greatest in Reach 1 and decreased in upstream reaches. The percentage of silt and sand increased

Table 5. Percent substrate composition for the three study reaches of Nankoweap Creek, Grand Canyon, February and March 1990.

	Percent Composition, by Reach		
Substrate	#1	#2	#3
Silt	1.25	1.14	4.75
Sand	9.06	16.36	18.25
Gravel	58.13	41.82	24.25
Cobble	18.44	18.18	10.25
Boulder	15.00	21.82	13.25
Armored	0.00	0.00	32.50
Vegetation	trace	0.91	trace
n	16	22	20

in Reach 3, as did the percent of armoring (33%).

The amount of pool habitat increased from Reach 1 to Reach 3. Pools in Reach 1 were fewer and had smaller volume than in Reach 2 and 3. Pools in Reach 3 were almost twice as large in volume than pools in Reach 1. Average pool depth also increased upstream (Table 6).

Average stream width decreased from Reach 1 and 2 to Reach 3. Reach 3 averaged 1.53 m wide while Reach 1 and 2 averaged 1.86 and 1.89 m, respectively.

During periods of low river discharge, the mouth of Nankoweap Creek flows through a series of small braided channels. These channels begin abruptly in the lower 20 meters of the creek. The creek near the mouth has one channel approximately 1.6 meters wide and abruptly divides into four channels 20 meters wide. The average depths of these channels range from 3.96 cm to 6.30 cm (Table 7). The substrate in these channels is predominantly gravel (65 %) with some cobble (20%), thereby allowing subsurface flow to further reduce surface flow. Shallow water, subsurface flow and steep gradient contribute to the impediments facing spawning trout attempting to move into Nankoweap Creek.

Trout Abundance and Spawning Phenology

Rainbow trout began moving into Nankoweap Creek in substantial numbers about February 12. After this date, the numbers of trout found in the creek increased steadily until the peak of abundance on March 2. On this evening, the total number

Table 6. Summary of pool morphology from all study reaches in Nankoweap Creek, Grand Canyon, February and March 1990. Standard deviations in parentheses.

Reach	Width (m)	Length (m)	Depth (cm)	Volume
1 n=6	1.72 (.65)	1.69 (.78)	16.00 (3.05)	0.47m^3
2 n=12	1.50 (.47)	1.88 (.53)	19.05 (5.05)	0.54m^3
3 n=14	1.62 (.38)	2.34 (1.21)	23.01 (4.52)	0.87m^3

Table 7. Average depth (cm) of braided channels exposed during low flow at the mouth of Nankoweap Creek, Colorado River, Grand Canyon, February and March 1990.

Channel	Depth (cm)	SD	n
Upstream #1	3.96	1.65	27
Upstream #2	4.30	3.14	30
Main channel #3	6.30	2.34	30
Downstream #4	4.13	3.35	30

of trout in the lower 600 m of the creek was 1565 individuals. From February 25 through March 5 trout in Nankoweap Creek numbered over 1000 fish. Trout abundance declined steadily after the peak (Fig. 12).

All rainbow trout observed during the six week study period were in spawning or post-spawning condition. During February, 97.7 to 94.6 % of all trout were in spawning condition. Post-spawning or "spent" fish increased in proportion to spawning fish (5.4 - 15.2%) after the peak abundance was observed in early March. The first spawning mortalities were observed in the week following the peak of trout abundance. Numbers of dead trout banks of the creek increased from 20-30 to over 100 by March 12 and moribund fish were observed beached in shallow areas. In addition to dead and dying trout, the number of trout with worn caudal, anal and ventral regions increased, possibly indicating the post-spawning condition of these fish.

Average size of rainbow trout collected during the study period was greatest in fish collected from the Colorado River at the mouth of Nankoweap Creek (362 mm) and smallest in Reach 3 (328 mm) of Nankoweap Creek (Table 8 and Fig. 13). Trout from Reach 1 and 2 were similar in size, 349 and 348 mm, respectively. Trout found in Nankoweap Creek were, on average, smaller (344 mm) than fish collected from the Colorado River at the mouth (Table 8 and Fig. 13).

Reach 3 was the only reach were a bimodal size distribution of trout was observed. While other reaches had a peak mode near 340

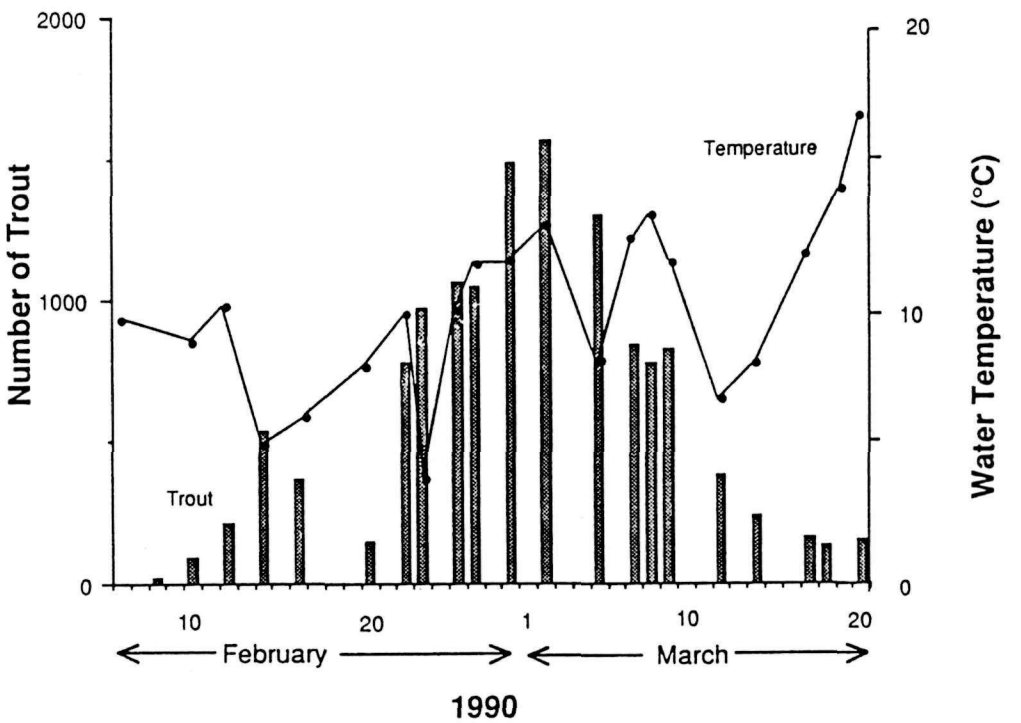


Figure 12. Water temperatures, dates, and abundance of rainbow trout at Nankoweap Creek, Grand Canyon, February and March 1990.

Table 8. Standard lengths (SL) in millimeters (mm) for rainbow trout sampled during February and March 1990 at Nankoweap Creek and its confluence with the Colorado River, Grand Canyon.

	Colorado River	Reach 1	Reach 2	Reach 3
n	466	308	253	175
Minimum	260	222	204	216
Maximum	445	445	436	493
Mean	363	349	348	328
SD	31.2	35.9	40.1	45.7

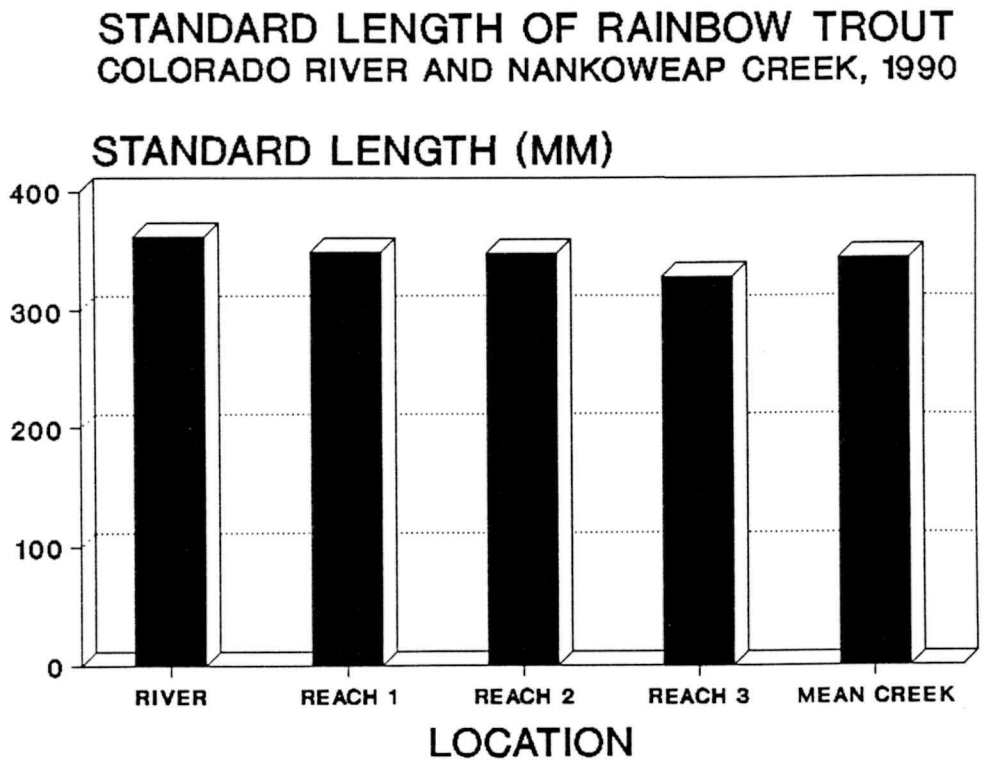


Figure 13. Average standard lengths of rainbow trout collected from Nankoweap Creek and the Colorado River during February-March 1990. (See Table 7 for detailed statistics.)

- 380 mm, Reach 3 had a peak at 260 - 280 mm and at 330 - 350 mm. These peaks probably represent two different age classes of fish (Bagenal 1987). The first fry were observed in Nankoweap Creek on March 8. These fish averaged 22 mm TL (n = 3, range = 18-25mm, SD = 3.6). Fry lengths at the end of the study period, about March 20 hadincreased to 27 mm (n = 8, range = 24 - 33mm, SD = 3.1). These recently emergent fry probably hatched from eggs fertilized 4 - 7 week prior, depending on stream temperatures during that period.

Trout Movement

Rates of movement of trout (fish per hour) into Nankoweap Creek showed no correlation with observed river flows (Fig. 14) but appeared to exhibit a slight correlation with stream temperature (Fig. 15; r = 0.40). Nighttime movements into the creek were greater than daytime movements (Fig. 16). Additional data under more extreme fluctuations may reveal other trends; stream temperature influences the timing of spawning runs of many species of salmonids (Scott and Crossman 1973, Sigler and Sigler 1987). The Nankoweap spawning run may be triggered when stream temperatures warm to a critical threshold level; as data indicate that creek temperatures above 7°C corresponded to the largest influx and abundance of trout into Nankoweap Creek (Figs. 12 and 15). Supporting evidence is also found during the period of February 14-20, when trout abundance dropped from 500 fish to near 100 fish after a sharp decline in stream temperature due to

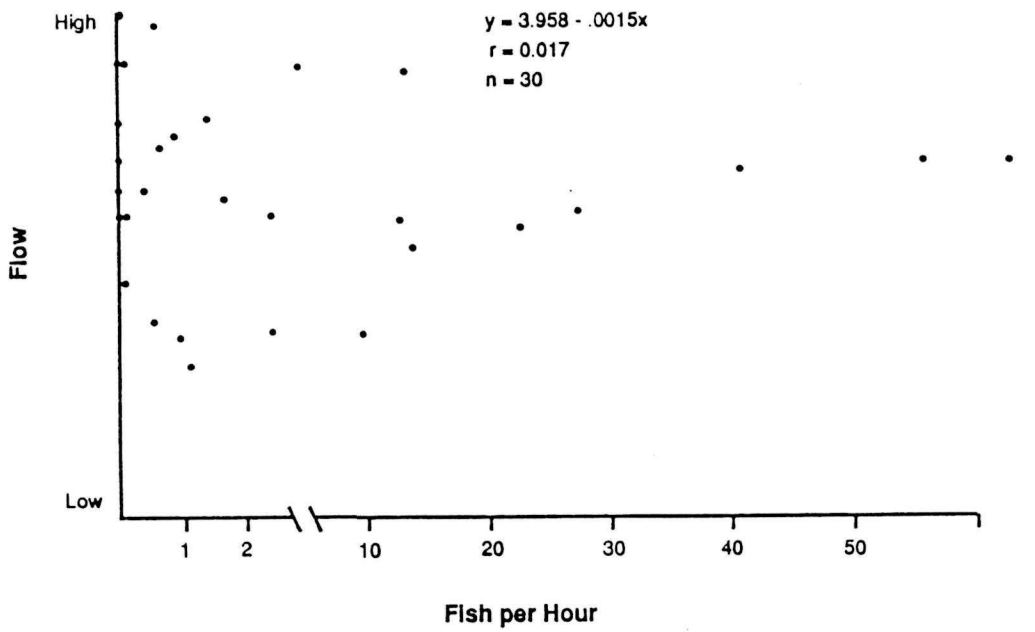


Figure 14. Rainbow trout movement into Nankoweap Creek under various flows in the Colorado River, February and March 1990.

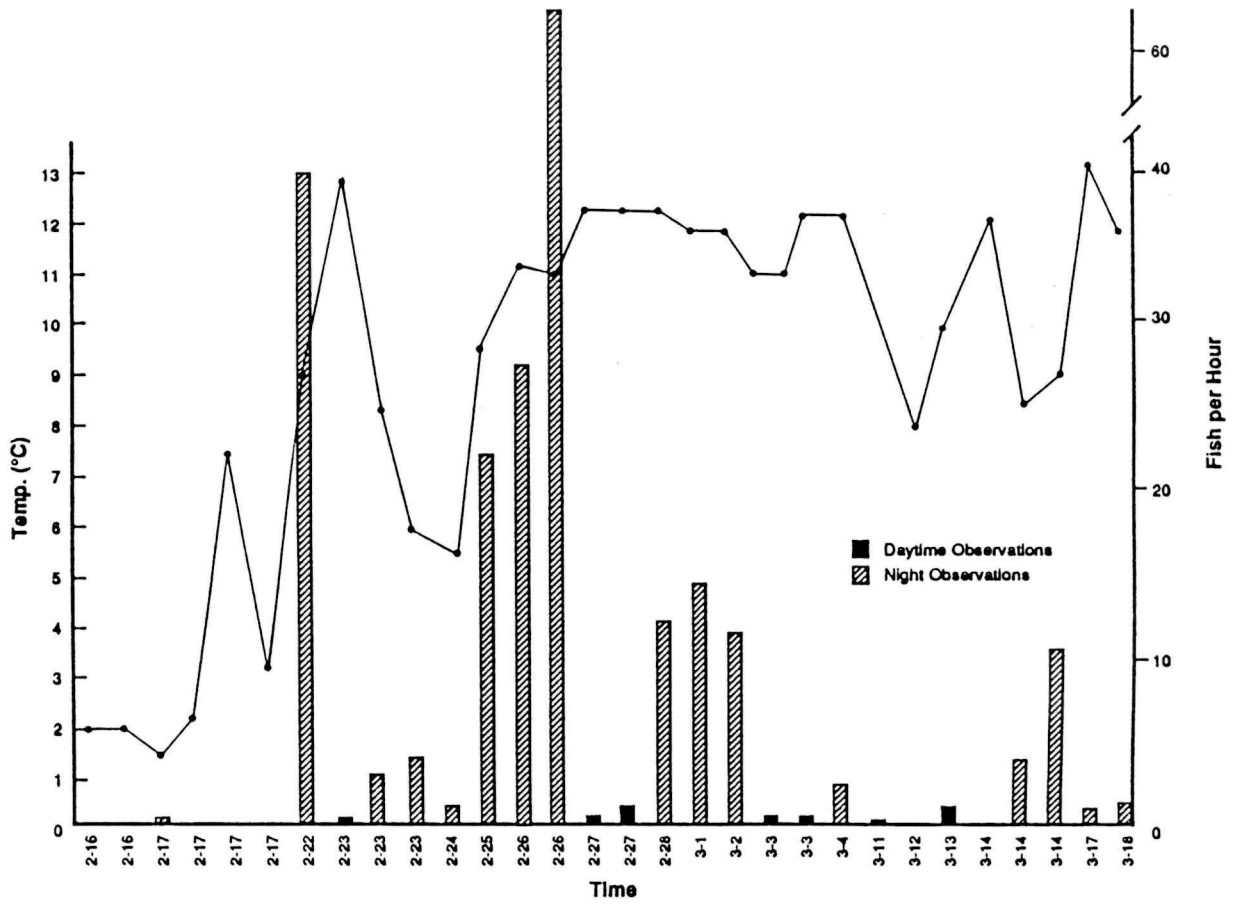


Figure 15. Numbers of rainbow trout entering Nankoweap Creek from the Colorado River under varying creek temperatures and flows in the Colorado River, Grand Canyon, February and March 1990.

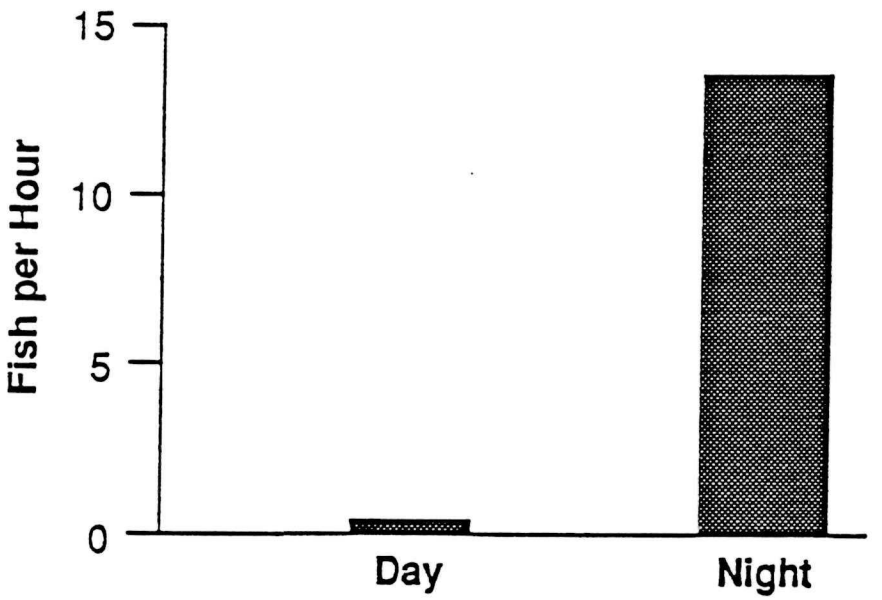


Figure 16. Day versus night movement of rainbow trout from the Colorado River into Nankoweap Creek, Grand Canyon, February and March 1990.

a winter storm (Fig. 12). The daily water temperature range during this period was actually from below 0°C to about 8°C, with many hours below 3°C. As ambient air temperatures rose so did creek temperatures followed by an increase in numbers of trout moving into the creek (Figs. 12 and 15).

It was not possible to observe trout moving into Nankoweap Creek at all possible flow regimes. Trout appeared to attempt to move into the creek in distinct pulses. Although there were times when fish were not moving into the creek, even during high river flows, there were also times that trout moved across 15 - 20 m of gravels covered by extremely shallow water. There was no indication that trout were prohibited from entering Nankoweap Creek at any observed flows.

Numbers of trout tagged from the Colorado River and recaptured in Nankoweap Creek were significantly correlated with discharges from Glen Canyon Dam (Fig. 17; $P = 0.003$, $DF = 17$, $r = 0.64$, $n = 19$). The data in Figure 17 are expressed as a percent of tagged fish recaptured to account for additional tagged fish released into the river during the study. At intermediate and high flows, a greater number of river tagged fish were recaptured in Nankoweap creek than at low flows (Figure 17). Trout moving into Nankoweap Creek under low flows demonstrate that fish can enter the creek at least down to these flows.

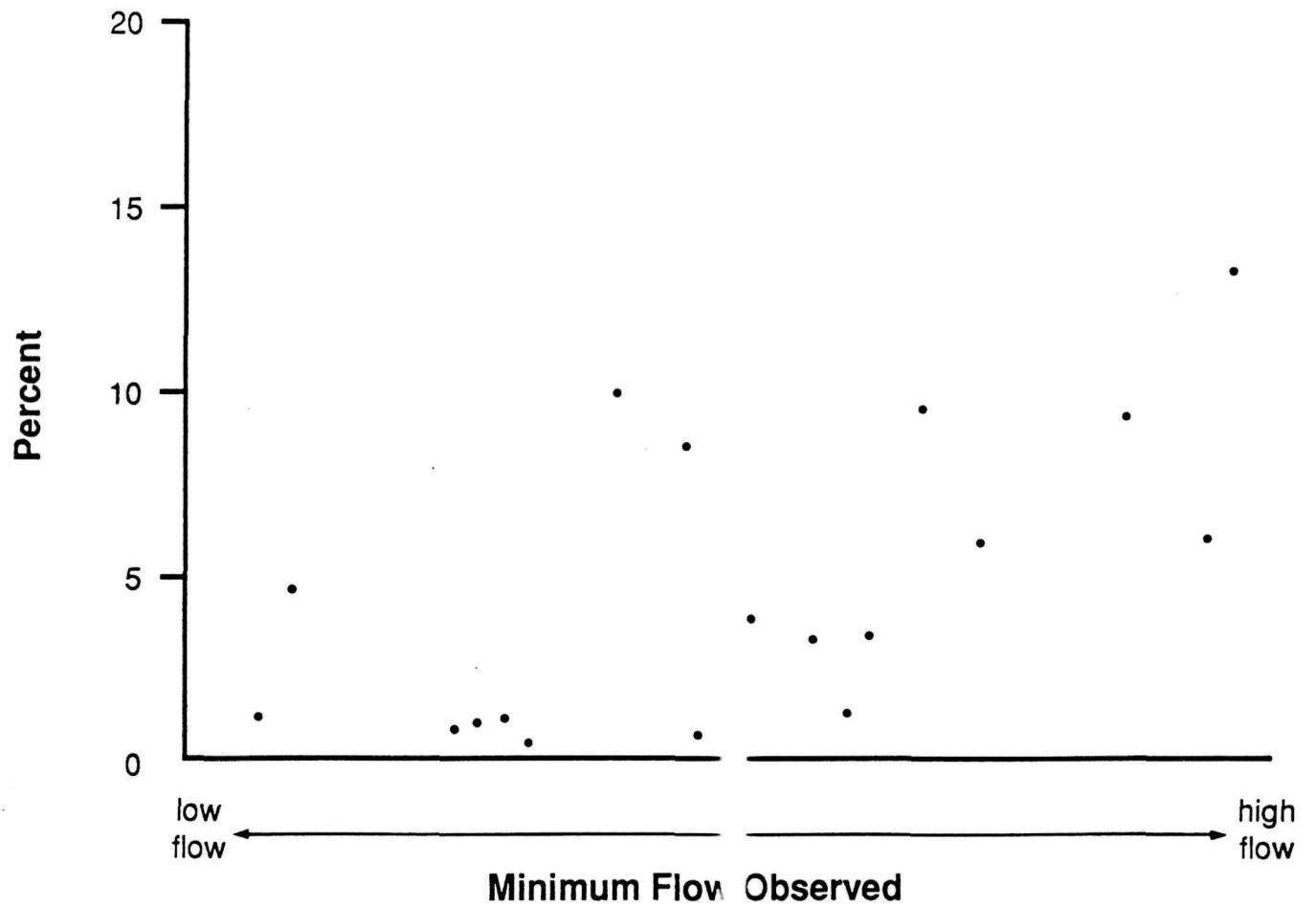


Figure 17. Percent of rainbow trout tagged in the Colorado River that were recaptured in Nankoweap Creek by minimum flows observed at the time of recapture, Grand Canyon, February and March 1990. (P=0.003, R=0.64, n=19)

Trout Residence Time in Nankoweap Creek

Average residence time for a trout in Nankoweap Creek was 6 days (n = 507, range = 1 - 34 days). Trout spent an average of 2.4 days in Reach 1 (range = 1 - 26 days, n = 507), 2.3 days in Reach 2 (range = 1 - 25 days, n = 507) and 1.3 days in Reach 3 (range = 1 - 25 days, n = 507).

Trout spent most of their time in the reach in which they were originally tagged (Fig. 18). Trout tagged in Reach 1 spent 5.9 days in that reach and only 1.5 and 0.4 days in Reaches 2 and 3, respectively. These trout remained in the creek an average of 7.7 days (range = 2 - 34 days, n = 140). Reach 2 trout resided in Reach 2 for 4.7 days, Reach 1 for 1 day and Reach 3 for less than 1 day. Average time in Nankoweap Creek for Reach 2 fish was 5.6 days (range = 1 - 26 days, n = 135). Reach 3 tagged trout spent an average of 6 days in Reach 3, 1 day in Reach 2 and less than 1 day in Reach 1. Total residence time of rainbow trout in Nankoweap Creek was 7.4 days (range = 1 - 25 days, n = 88).

Trout originally tagged in the Colorado River and recaptured in Nankoweap Creek spent an average of 4 days (n = 143, range 1 - 19 days) in the creek. Once they entered the creek, these fish spent most of their time in Reaches 1 and 2 (1.7 and 1.6 days). Only 0.5 day was spent in Reach 3 (Fig. 18).

The relative distribution of rainbow trout within each reach varied over the period of study (Fig. 19). Initially, most trout inhabited Reach 1, but by the third week of observations, trout were more numerous in Reach 2. Numbers of trout in Reach 3

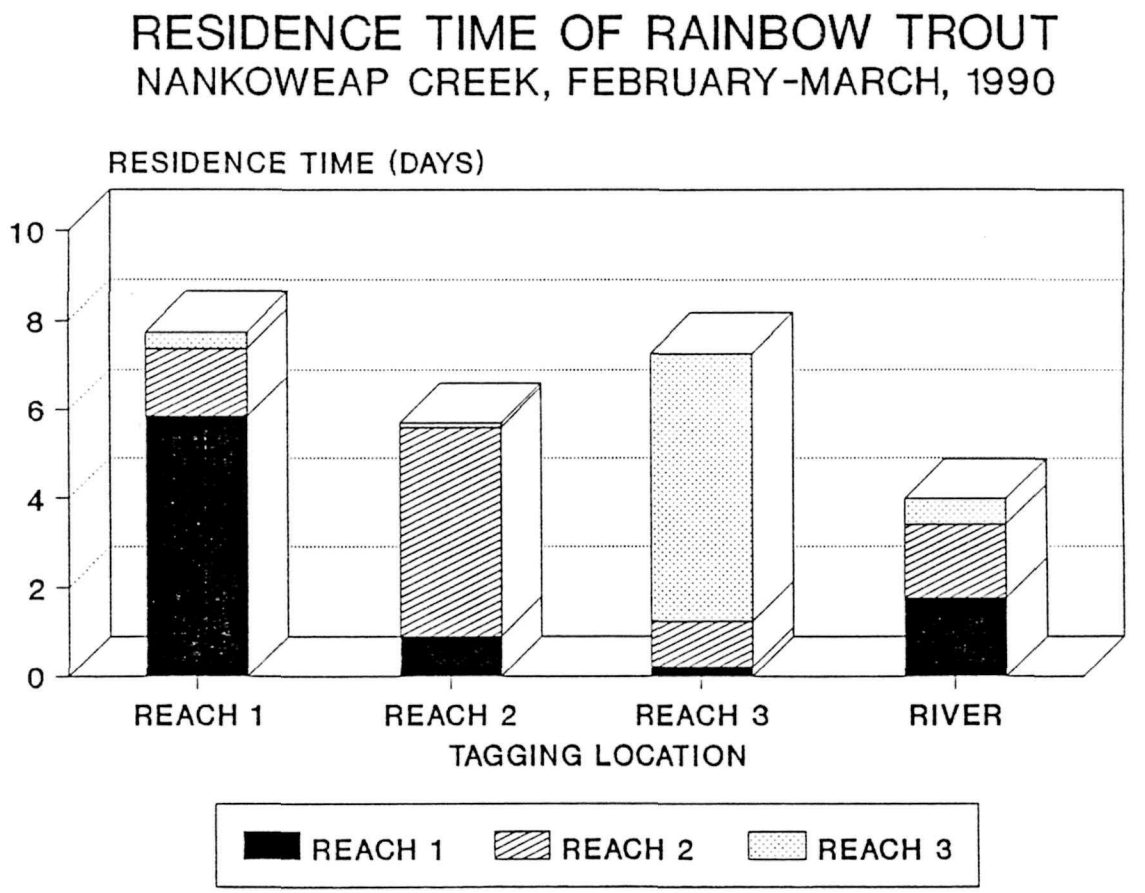


Figure 18. Average residence time of rainbow trout (n = 507) in each study reach in Nankoweap Creek by original tagging location, Grand Canyon, February and March 1990.

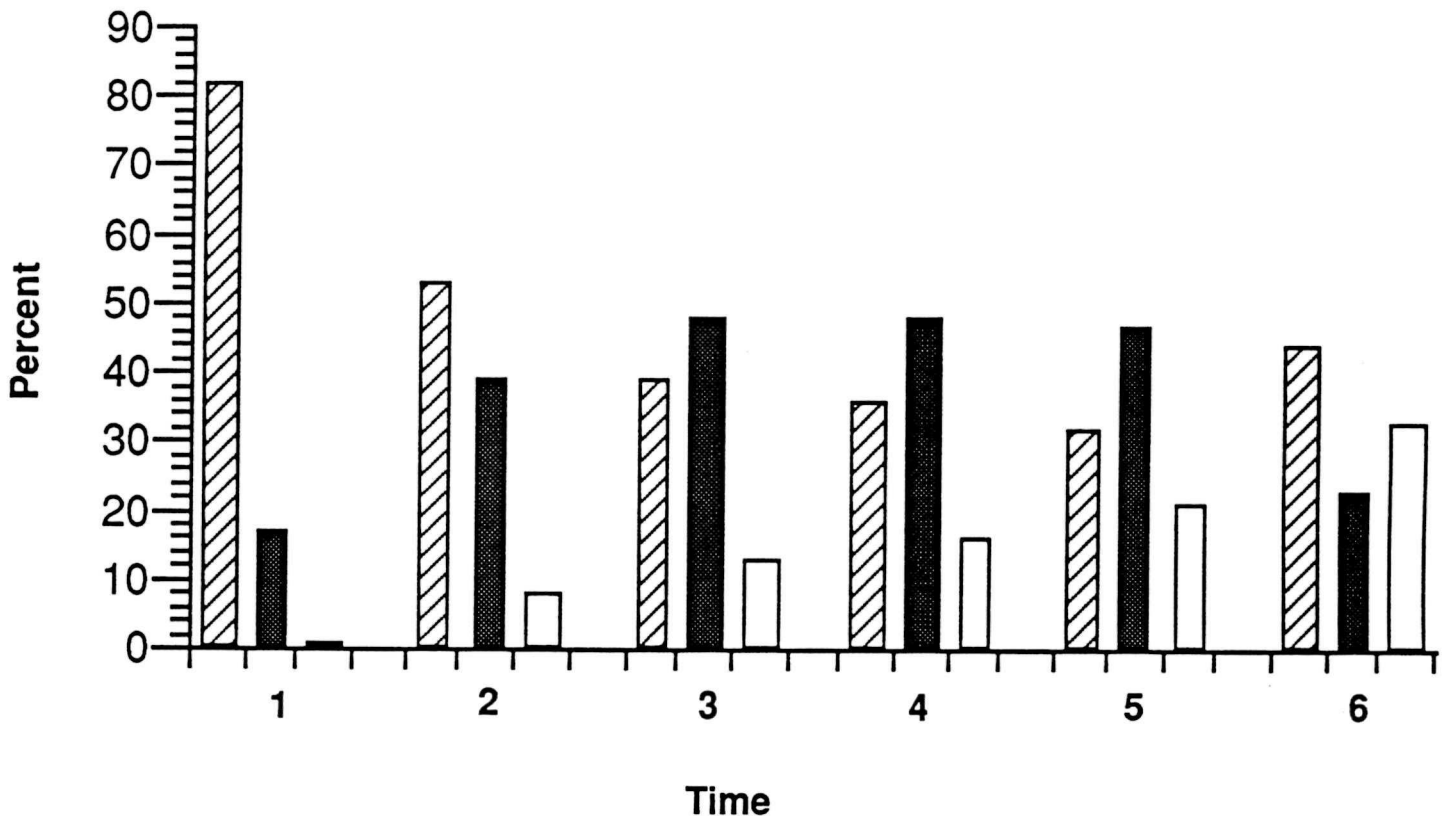


Figure 19. Relative distribution of rainbow trout in each study reach in Nankoweap Creek, Grand Canyon, at weekly intervals during February-March 1990. Reach 1 = slashed bars, Reach 2 = stippled bars, Reach 3 = open bars.

increased steadily throughout the study period, from 1% in week one to 33% at week 6 (Fig. 19).

DISCUSSION

Avian Ecology

Abundance and Timing of the Eagle Concentration

The wintering and migrating bald eagles at and near the mouth of Nankoweap Creek represent the largest, regularly occurring winter concentration of eagles in the Southwest. No comparable concentration of eagles occurs in Arizona or New Mexico (pers. comm., T. Tibbitts, Arizona Game and Fish Dept.; pers. comm., J. Hubbard, New Mexico Game and Fish Dept.). For the purpose of this study, an eagle concentration is defined as an area of 1 km^2 or less where more than 10 individuals occur on a daily basis for at least 2 weeks.

Eagle abundance appears to be related, in part, to the abundance of trout in the creek. Increasing numbers of eagles at Nankoweap in 1990 coincided with the increasing abundance of spawning through late February (Fig. 3). Reasons for the sharp decline in eagle abundance after March 1, even though trout abundance continued to remain high, are not fully understood. However, the decline may be due to a combination of several factors.

First, the eagles' innate migratory urge may have caused them to leave Nankoweap and begin their return migration to nesting areas in the Pacific Northwest, even though abundant food

resources were still available at Nankoweap. Information on the spring chronology of bald eagle migration in the Southwest is lacking, making this hypothesis difficult to test. Secondly, increasing levels of human disturbance after March 5 may have caused many eagles to prematurely abandon the area for the season. Human disturbance, in the form of rafters and hikers, occurred an average of once every 2.9 days from February 7 through March 5; while human disturbance occurred an average of once every 1.5 days from March 6 to 20. Recreational boating and hiking activities have been shown to adversely affect bald eagle behavior, distribution, and food intake (Stalmaster and Newman 1978, Knight and Knight 1984). Human disturbance to wintering or migrating eagles has been studied exclusively under conditions of dispersed food resources; the effects of human disturbance on eagles at a concentrated food resource, such as spawning trout at Nankoweap, potentially could be more severe.

The data on hand concerning the timing and abundance of the eagles at Nankoweap suggests that the eagles concentrate there immediately prior to their return migration to nesting areas in the Pacific Northwest. This hypothesis will require further testing in 1991 before it can be confirmed. The following scenario describes the hypothesis that will be tested.

Migrant eagles from the Pacific Northwest apparently begin to move into and through the Grand Canyon region in November, with most individuals continuing on to overwinter in central and southern Arizona and northwest Mexico. The trout spawn at

Nankoweap appears to be highly variable from November through early February (H. Maddux, pers. comm.). The food resource, then, may not be sufficient to provide the prey base required to concentrate eagles at Nankoweap throughout the entire winter. The variable trout spawn is opportunistically exploited by the relatively small numbers of eagles that overwinter along the Colorado River in northern Arizona. Preliminary data from Lake Powell in the Glen Canyon National Recreation Area on the Arizona/Utah border suggest that the peak abundance of wintering eagles takes place in early January (Kline 1990).

Trout abundance in Nankoweap Creek begins to increase as late winter temperatures increase. This increase coincides with the beginning of northward migration by bald eagles located to the south of Grand Canyon. At this time, eagles that have previously become accustomed to exploiting the trout spawn at Nankoweap begin to move into the study area, and are joined by ever-increasing numbers of eagles that may have discovered the site by chance or by following other eagles to it. These eagles are using Nankoweap as migratory stopover resting and feeding habitat, and as a staging area prior to the initiation of their final northward migration.

Eagle abundance increases from early February through approximately late February or early March. The exact timing of the peak of the eagle concentration depends on the timing of the trout spawn, the eagles' innate migratory urge, weather, and possibly the levels of human disturbance in the study area. At

this point, the number of eagles departing from Nankoweap on their northward migration exceeds the number of eagles arriving from the south, and the concentration diminishes. By mid-March, few eagles remain and they, too, leave the region by early April.

The reasons for the eagle concentration at Nankoweap are analogous to those that caused the bald eagle concentration along McDonald Creek in Glacier National Park, Montana (McClelland 1973). There, an autumn run of introduced Kokanee salmon (Oncorhynchus nerka) was responsible for the largest concentration of migrating bald eagles in the contiguous 48 United States. The timing of the salmon spawning run at Glacier National Park coincided exactly with the initiation of southward eagle migration, allowing the eagles to use the area as a staging area at which to feed prior to continuing their migration.

Eagle Time and Activity Budget

Generalized activities of Nankoweap eagles exhibited patterns similar to those reported for wintering eagles in Washington (Stalmaster and Gessaman 1984) and Connecticut (Craig et al. 1988). Most of the daytime was spent perching, the least energetically expensive activity over a wide temperature range and the strategy that minimized conductive and convective heat loss (Calder and King 1974). This strategy of inactivity minimizes energetically expensive activity at a time when conditions for survival are suboptimal (Stalmaster and Gessaman 1984, Craig et al. 1988). Nonflight activities occupied 96.9% of

the daytime in Washington, 90.2% of the daytime in Connecticut, and 89.8% of the daytime at Nankoweap. Eagles may be more active at Nankoweap because of the warmer climate; because they may be under less energetic stress due to abundant, easily available food resources; and because they are apparently staging for migration and may be experiencing migratory restlessness.

Subadult and immature eagles at Nankoweap spent generally less time perching, more time in active and passive flight, and more time feeding than did adults, in a pattern similar to that seen in juvenile eagles in Connecticut (Craig et al. 1988). Greater energy expenditure by young eagles may be disadvantageous (Craig et al. 1988), and is apparently a result of their inexperience and social subordination (Knight and Knight 1983, Stalmaster and Gessaman 1984). Inexperience may be less meaningful, however, in a situation such as Nankoweap, where prey is evidently abundant and easily accessible. Likewise, social subordination may be more a function of size than age (Garcelon 1990). Adults at Nankoweap spend more time waiting to feed than subadults or immatures, the opposite of that observed in Connecticut (Craig et al. 1988).

Foraging Ecology

The mouth of Nankoweap Creek and that area within 50 m of the confluence constituted the most important foraging habitat for bald eagles, based on the large proportion of foraging events we observed there. Most of this locale was subject to daily

inundation and exposure by fluctuating flows during the study period.

The morning and afternoon peaks of eagle foraging activity (Fig. 4B) corresponded almost identically to the daily bimodal peaks of foraging activity described by Haywood and Ohmart (1986) for nesting bald eagles in Arizona.

Subadult and immature eagles foraged primarily in the creek (Table 2), where overall foraging success was very high (Table 3). Foraging in the creek, then, was advantageous to younger eagles which were less experienced at obtaining prey. Adult eagles exploited a wider variety of foraging locations as compared to the younger age classes, presumably due to their greater experience and higher rate of foraging success for all localities with an adequate sample size for comparison.

Foraging events in the river were much less successful for all age classes than creek forages (Table 3). This difference may partially account for the relatively small proportion of foraging events in the river (Table 2). Although foraging success for live trout stranded by fluctuating flows in isolated pools was the highest for any foraging habitat (Table 3), isolated pool forages were infrequent and comprised only 5% of the total foraging events (Table 2).

Wintering bald eagles are often food limited (Sherrod et al. 1976, Stalmaster and Gessaman 1984). Therefore, the trout spawn at Nankoweap Creek, with its abundance of easily-accessible prey, is of great benefit to the relatively large number of eagles that

encounter it. Food limitation has potentially greater consequences for younger eagles, which are less experienced at obtaining prey and engage in a greater proportion of energetically-expensive activity. An opportunity to gorge on trout at Nankoweap before the rigors of northward migration would potentially increase survivorship of young eagles.

The proportion of adults to younger individuals at the peak of the eagle concentration at Nankoweap in 1990 was 1:1.6. This is a substantially greater proportion of young eagles than the average North American ratio of adults to younger individuals of approximately 1:0.6 (Millsap 1986). Young eagles occurred at Nankoweap in greater proportions that would have been predicted by chance alone, possibly as a result of the abundance and availability of prey. If food is the most important limiting factor on survivorship, particularly of younger eagles (Sherrod et al. 1976, Stalmaster and Gessaman 1984, Griffin and Baskett 1985), then management strategies that help to maximize food intake of immatures in winter may aid in the recovery of regionwide eagle populations (Stalmaster and Gessaman 1984).

Energetic Simulation Model

The 26,937.2 kcal provided to the eagle population by fluctuating flows was enough to meet the daily energy requirements of 59.2 eagles for one day (59.2 eagle-days), at the mean caloric expenditure rate of 455.2 kcal/day. Whether or not eagles would have exploited alternate prey (more live trout from

the creek, for example) to compensate for the lack of prey in isolated pools if fluctuations had not occurred is unknown. This possibility will be tested in 1991 if the appropriate experimental flow regimes occur during the study period.

The energetic surplus of 16,954.2 kcal was less than the 26,937.2 kcal contributed by the effects of fluctuating flows, indicating that the eagle population would have exhibited a 5% energetic deficit without the prey items contributed by fluctuating flows. Therefore, the 6% energetic surplus apparently existed because of the effects of fluctuating flows. This surplus was theoretically converted to fat by the eagle population, presumably to prepare eagles for the rigors of migration. The opportunity for migrating bald eagles to put on fat immediately prior to their northward migration would be a distinct advantage for those individuals encountering the trout spawn at Nankoweap Creek. The extent of this advantage, with speculations on its consequences, will be explored in more detail in future phases of this study.

Some input variables to the energetic simulation model may have caused inaccuracies in model results. For example, the edibility quotient of trout, the competition factor, and the kcal/g of edible trout biomass was after that reported by Stalmaster (1983) for coho salmon. Furthermore, weather data were not obtained on site but from weather stations at different elevations within 50 km of the study area. These variables will all be measured in the field during the 1991 study period.

Effect of Fluctuating Flows on Eagle Food Intake and Foraging Patterns

Eagle caloric intake is indirectly influenced by fluctuating flows that strand live and carrion trout in isolated pools where they can be easily captured by eagles. This influence of fluctuating flows is slightly positive (11.5% of all prey items consumed, 11% of all kcal consumed), resulting in a daily energetic budget for eagles that was 6% surplus instead of 5% deficit.

The highly significant shift in eagle foraging patterns resulting from strongly fluctuating flows indicates that dam operation can influence eagle behavior. This shift in foraging patterns was evidently not related to the distribution of prey; Figure 19 indicates that trout were distributed throughout the lower 500 m of the creek during most of the eagle concentration.

The influence of fluctuating flows on foraging patterns takes place because of changing conditions in foraging habitat, changes that may be related to the availability of prey. Prey availability was not documented during the study period, but will be quantified during the 1991 study period. Changing conditions in foraging habitat due to fluctuating flows may have caloric consequences for eagles. Foraging success in the creek, for example, was higher upcreek than at its mouth, although the majority of foraging events occurred at the mouth (Fig. 5). The hypothesis that changing conditions in foraging habitat due to

fluctuating flows do not have caloric consequences for eagles will also be tested during the 1991 study period.

Aquatic Ecology

Spawning rainbow trout are influenced by a complex of factors that control spawning movements and behavior (Scott and Crossman 1973). As in other salmonids, rainbow trout spawn in the tributaries of larger rivers or lakes. The primary triggering mechanism that initiates spawning migrations is the temperature of the tributary. Naiman et al. (1987) among others, suggest that salmonids move into sidestreams when mainstream temperatures equal tributary temperatures. In Nankoweap Creek, this same pattern was observed during February 1990, when trout abundance increased dramatically as creek temperatures equalled river temperatures (Fig. 12). In January 1989, water temperatures in Nankoweap Creek were never above 1°C, and trout abundance was fewer than 10 fish for the entire week of observations (Brown et al. 1989a).

Local weather patterns may control tributary water temperatures in the Grand Canyon, especially Nankoweap Creek. Streams of low discharge that flow through open valleys have highly variable water temperatures that fluctuate with ambient air temperatures (Hynes 1970, Usher et al. 1984). With increasing distance away from their sources, these streams show a pronounced positive correlation with ambient air temperatures. Data from Usher et al. (1984), from both North Rim and South Rim

tributaries, indicate how stream temperatures become extremely variable with distance from their spring source. These variations in stream water temperatures with weather patterns may cause spawning migrations to take place at different times from year to year.

Observations of spawning aggregations in Nankoweap Creek over the past seven years support the fact that trout can spawn any time from December through March (Unpubl. Arizona Game and Fish Department data from Nankoweap Creek 1984-86, Maddux et al. 1987). Although spawning aggregations, egg deposition, and fry emergence are documented for Nankoweap Creek (Maddux et al. 1987, Kondolf et al. 1989) successful recruitment into the mainstream fish population has not been documented.

Rainbow trout fry observed in late February in Nankoweap Creek had hatched from eggs that were fertilized approximately 4 - 7 weeks prior. Length of time to hatching is dependent on stream temperatures, with colder temperatures resulting in longer time to hatching (Scott and Crossman 1973).

Fish movements into Nankoweap Creek during February and March 1990 appear to be controlled primarily by water temperature. A moderate correlation exists between fish per hour moving into Nankoweap Creek and increasing water temperature (Fig. 15). Total trout abundance in Nankoweap Creek increased with stream temperature during the month of February until the peak of abundance. At this time stream temperatures continued to rise as the spawning activity waned. As stream temperatures approached

16-17 °C, above preferred spawning temperatures of 10-12°C, (Scott and Crossman 1973), abundance of trout declined (Fig. 12). At this time it is unknown whether temperature caused this decline or spawning activity declined on its own. Increased spawning mortalities observed after the peak of abundance may indicate that the spawn was waning and temperature was not responsible for the decline in trout numbers.

A confounding factor that appeared to occur frequently was that spawning movements were sporadic and intermittent. During some observation periods, trout were moving into Nankoweap Creek regardless of river levels. At other times, under similar discharges, no fish were observed. Increased sample sizes through additional data collection will overcome this problem.

Numbers of fish moving into Nankoweap Creek varied between 0 and 62 fish per hour during the study period (Fig. 15). Never, under any flow regimes released during this study, were trout prohibited access to Nankoweap Creek. Even while river flows were low, exposing a large gravel bar at the mouth of Nankoweap Creek, trout were observed moving freely into the creek. As flow levels increased and covered this gravel bar it appeared that trout had easier access to the creek proper.

The number of trout tagged in the river recaptured in Nankoweap Creek was significantly correlated with river flow (Fig. 17). As minimum daily discharges increased, more river tagged fish were recaptured in Nankoweap Creek. Although fish were observed moving into Nankoweap Creek at the low flows, at

intermediate and high flows the number of recaptured fish in Nankoweap Creek rose steadily.

Although these data are only for fish recaptured in Nankoweap Creek, they can be interpreted as movement data as well. Days with low minimum flows had medium to high flows at least part of the day, but days with higher minimum flows had more hours at higher flows, that would have made access to the creek less difficult (Fig. 1). Therefore, fish may have been staging at the creek mouth until river discharges rose to allow easier access to Nankoweap Creek. This indirect method of estimating fish movements combined with the method of direct observations of fish per hour may allow for more accurate analysis of effects of flows on trout movement into Nankoweap Creek.

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