

TEMPORAL VARIATION IN PREY PREFERENCE PATTERNS OF ADULT OSPREYS

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ABSTRACT.—I examined temporal variation in diet with respect to fish dynamics in a resident population of Ospreys (*Pandion haliaetus*) in Florida for 18 months. Bass (*Micropterus salmoides*, *Morone saxtilis*) were captured in proportion to their abundance. Ospreys exhibited preference for sunfish (*Lepomis* spp.) from May to August 1985 and from March to July 1986. Shad (*Dorosoma* spp.) were preferred from September to February. These shifts were closely related to concurrent shifts in sunfish abundance; preference for sunfish was exhibited when they were most abundant. When sunfish abundance declined, Ospreys switched back to shad. Shifts from shad to sunfish also were associated with a switch in foraging habitat. Ospreys hunted preferentially in the littoral zone of the lake during peak abundances of sunfish and foraged in the limnetic zone when concentrating on shad. Changes in preference for sunfish lagged 1.2 months behind changes in sunfish abundance, but lagged less than 0.3 months for shad. Variation in sunfish abundance was greater than that for shad, suggesting that the ability of Ospreys to exhibit strict concordance between abundance and preference may depend on the amplitude of the change in abundance. Received 6 July 1987, accepted 11 November 1987.

FORAGING studies of birds often concentrate on discrete time periods (e.g. nonbreeding season, Craig 1978; winter vs. summer, Baker and Baker 1973, Opdam 1975). This approach risks the potential loss of information on temporal aspects of foraging, in particular how diet choice is affected by annual cycles in the abundance of particular prey types or annual stages in predator life histories (e.g. brood rearing, post-fledging). Relationships between diet and these two temporal factors would be apparent only by year-round study of the same population of predators.

I studied the influence of variation in resource availability and annual stages such as breeding on diet choice in a resident population of Ospreys (*Pandion haliaetus*) in north-central Florida. First, I examined the effects of temporal change in the available fish resource base on diet choice by Ospreys. Numerous foraging models imply a switch by predators from a generalist to specialist strategy as prey abundance increases (references given by Pyke 1984). I also determined whether Ospreys responded immediately to changes in prey availability, as

suggested by a "two-armed bandit" model (Krebs et al. 1978), or exhibited a time lag in response while new search images were being developed (Hughes 1979).

Last, I tested whether a relationship exists between preference for particular prey types and annual stages in Osprey life history. For example, strong preference for one prey type before breeding may indicate a need for "nutrient-rich" prey (Pulliam 1975, Westoby 1978) for egg formation, while change in preference after young hatch may reflect different nutrient requirements for growing young.

METHODS

Study area.—I conducted my research on Newnan's Lake, Alachua Co., Florida, from March 1985 to September 1986. Newnan's Lake, located 15 km east of Gainesville, is a shallow (1–3 m depth), 2,400-ha hypereutrophic lake (Shannon and Brezonik 1972) rimmed with baldcypress (*Taxodium distichum*) and mixed hardwoods. The shallow structure of the lake allows vegetation to establish roots in part of the underlying substrate, creating a littoral (rooted vegetation present) and limnetic (rooted vegetation absent) zone. The presence of two lake habitats, the littoral and limnetic zones, affects the fish resource base and presents two different foraging habitats.

Evaluation of prey base.—I used electrofishing (see review by Reynolds 1983) to estimate fish availability on a monthly basis. One advantage of electrofishing

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is that it samples fish at or near the top of the water column. Fish sampled thus represent what is available to Ospreys, which cannot dive to great depths to capture prey. I assumed that variation in fish availability was negligible between daily sampling periods and that the number of prey consumed by Ospreys at Newnan's Lake was small relative to the number of fish available.

Twelve 15-min electrofishing transects, six each in the littoral and limnetic zones, were run on two consecutive days in each month. Trends in fish abundance were based on the number captured per 15-min transect. Fish were identified to species, and mass (g) and length (cm) were measured. I excluded from analysis unlikely prey for Ospreys (e.g. bottom-dwelling brown bullhead, *Ictalurus nebulosus*; and Florida gar, *Lepisosteus platostomus*) because I felt their inclusion would bias results by inflating preference measures for other prey types. I combined prey into three categories: bass (largemouth bass, *Micropterus salmoides*; striped bass, *Morone saxatilis*); sunfish (warmouth, *Lepomis gulosus*; bluegill, *L. macrochirus*; redear sunfish, *L. microlophus*); and shad (gizzard shad, *Dorosoma cepedianum*; threadfin shad, *D. petenense*). Prey species were combined for two reasons. First, the fish species placed together are similar behaviorally and ecologically (Minckley and Krumholz 1960; Breder and Rosen 1966; Childers 1967; Carlander 1969, 1977). Second, and more important, body forms of grouped fish species are similar, and Ospreys probably cannot distinguish minute differences (e.g. presence of red dot on lateral surface of redear sunfish) between species in the absence of gross behavioral differences.

Osprey foraging behavior.—I observed Osprey foraging behavior from a boat anchored offshore at locations that facilitated simultaneous observations of several birds. The numbers of observable Ospreys ranged from roughly 40 birds during the winter months to more than 100 during the summer months. Individual Ospreys were watched until the completion of a 15-min period or until a successful capture was made and the fish type and size determined. I preferred this approach over continuous observations because of difficulties associated with maintaining observation of the same individual, and because it increased the number of independent samples. Although it has been suggested that foraging behavior ultimately must be analyzed at the individual level (Chesson 1984), logistical constraints precluded capturing and color-marking large numbers of adult Ospreys. Consequently, my results should be viewed at a population rather than individual level. Sexes were distinguished on the basis of plumage characteristics (MacNamara 1972).

I collected data during two 5-day periods, one before and one after the 2-day interval during which fish were sampled. Because of small sample sizes relative to the number of classifying variables, I collapsed data from each observation day into monthly

periods centered about each electrofishing sample. The species of fish captured by Ospreys were identified from silhouettes and were assigned to one of three 10-cm size classes (10–20 cm, 20–30 cm, 30–40 cm) based on the length of the fish relative to the bird (see Poole 1982). The approximate location and habitat type associated with each capture was noted on 7.5-min U.S. Geological Survey topographic maps.

Analysis.—I used log-linear analysis to develop statistical models that describe Osprey use of the available fish resource base over time (see also Heisey 1985). Log-linear analysis is similar to analysis of variance for use on multidimensional categorical data (Bishop et al. 1975, Feinberg 1980, Agresti 1984). Hereafter, "factor" refers to the variables of interest, "level" to categories within each factor, and "cell" to the intersection of more than two levels. Factors analyzed included prey type (F), prey size class (C), time (T; by month), habitat (H; littoral or limnetic), and Osprey sex (S).

Model cells containing the number of each prey type and size class captured by Ospreys were weighted by the relative abundance of each fish species and size class before analysis. Weighting standardizes the cell expected value to its estimated frequency in the environment. For example, fish species comprising 10% and 90% of the resource base should not have identical (i.e. 0.5) expected capture probabilities if Ospreys forage at random. Instead, capture data must be standardized to the relative probability of encounter of each fish species (here, 0.1 and 0.9, respectively). A similar approach was used to weight the analysis of foraging habitat.

I evaluated first all possible models using the likelihood ratio statistic, G^2 , eliminating those with significant P -values. When several statistical models of increasing complexity (i.e. more factors) fit the data, conditional tests (Agresti 1984: 57–58) were used to determine the best-fit model. This approach subtracts G^2 -values and degrees of freedom of more complex from less complex models to determine whether the more complex model adds additional information. A significant G^2 -value suggests that the more complex model adds additional information and should be considered.

Once a best-fit model was chosen, I calculated lambda estimates for each cell in the model. Lambda estimates measure the difference between expected and observed values (i.e. cell residuals), and they can be used as a measure of preference for a particular fish species and size class (i.e. positive estimates suggest use at a rate greater than expected if foraging was random). I considered significant positive lambda estimates to indicate "preference" for a particular fish resource type. Nonsignificant lambda estimates indicated random use. Comparisons of lambda estimates and construction of confidence intervals were made using formulas provided by Manly (1974) and Heisey (1985). Methods described by Bulmer (1974) were used

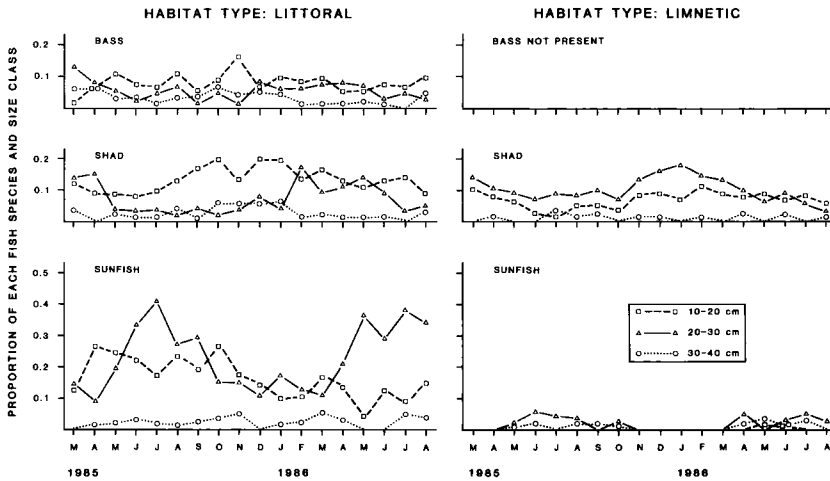


Fig. 1. Relative abundance of each fish species in littoral and limnetic habitat. Patterns presented also generally reflect change in fish absolute abundances. See text for fish species and size classes that differ.

to determine the extent to which preference patterns lagged behind changes in fish abundance.

The level of significance for all analyses was 0.05 unless otherwise noted. All analyses were performed using procedures found in Biomedical Computer Programs (BMDP-4F; Dixon 1985), Statistical Analysis Systems (CATMOD; SAS Inst. 1982), and Statistical Package for the Social Sciences (LOGLINEAR; SSP5x 1986) analytical guides.

RESULTS

PREY BASE DYNAMICS

Prey relative abundances varied by fish species, size class, time, and especially lake habitat (Fig. 1). Bass were never observed in the limnetic zone, and sunfish were found there only seasonally. In the littoral zone bass abundance was constant over time within each size class. Shad were found in approximately the same overall proportions in limnetic and littoral habitats, although 10–20-cm-size shad were more prevalent in the littoral than limnetic zone (Fig. 1). Shad in the 30–40-cm range were uncommon in both habitats. Unlike bass, the shad population appeared to cycle, with high winter and low summer abundances.

Sunfish dynamics differed from those of bass and shad. Sunfish were always present in the littoral zone but were observed only seasonally in the limnetic zone (Fig. 1). In the littoral habitat 20–30-cm sunfish exhibited a cyclic pattern that peaked between May and August. Smaller,

10–20-cm sunfish did not cycle, although their abundances decreased throughout the study period. Whether this decrease represents a longer cycle is not known. Abundances of 30–40-cm sunfish were constant and low over time. Sunfish also exhibited two brief, distinct movements into the limnetic zone. Patterns of change in absolute abundance were generally similar to those exhibited for relative abundance, and can be inferred from Fig. 1.

To determine whether variation was constant through time for each fish group and size class, I applied Levene's test for homogeneity (Milliken and Johnson 1984: 19–23) to the monthly electrofishing samples. All fish species and size class combinations in the littoral habitat and all combinations but one in the limnetic habitat exhibited significant differences in variance over time ($F_{17,90} > 4.23$ for each combination, $P < 0.05$). Only 20–30-cm shad had homogeneous variance over time ($F_{17,90} = 1.48$, $P > 0.05$).

OSPREY FORAGING PATTERNS

I observed 2,823 successful captures (roughly 15/observation day) during the 18-month study. Because of the high number of possible statistical models describing Osprey foraging, I first examined partial and marginal associations among the five factors, retaining only those terms with both a significant marginal and partial association (Brown 1976). Four of 10 possible 3-factor interactions (FCT, CHS, CHT, and

TABLE 1. Tests of partial and marginal associations among the factors prey type (F), prey size class (C), habitat (H), Osprey sex (S), and time (T). No 4-factor interaction terms had significant partial or marginal associations, and none are presented.

Effect	Partial association			Marginal association		
	df	G ²	P-value	df	G ²	P-value
2-factor terms						
FC	4	137.3	<0.001	4	47.3	<0.001
FH	1	0.2	0.738	1	3.9	0.049
FS	2	1.6	0.444	2	10.9	0.005
FT	34	176.7	<0.001	34	192.5	<0.001
CH	2	187.2	<0.001	2	57.8	<0.001
CS	2	58.8	<0.001	2	28.1	<0.001
CT	34	120.5	<0.001	34	121.0	<0.001
HS	1	42.3	<0.001	1	65.8	<0.001
HT	17	69.9	<0.001	17	109.8	<0.001
ST	17	743.5	<0.001	17	727.0	<0.001
3-factor terms						
FCH	1	0.6	0.438	1	2.8	0.091
FCS	4	4.5	0.341	4	3.4	0.492
FCT	61	146.7	<0.001	61	127.9	<0.001
FHS	— ^a			— ^a		
FHT	9	15.9	0.069	9	10.7	0.296
FST	34	37.6	0.307	34	45.3	0.093
CHS	2	21.5	<0.001	2	51.8	<0.001
CHT	29	54.9	0.002	29	58.9	0.008
CST	34	48.9	0.047	34	59.6	0.004
HST	17	17.9	0.390	17	20.2	0.265

^a Pattern of structural zeros causes negative df and precludes calculation of a reliable G² estimate.

CST) had significant partial and marginal associations and were retained (Table 1). No 4-factor terms had significant associations, while all 2-factor terms had at least one significant interaction.

A model containing the terms FCT, CHS, CHT, and CST represented the most complex but not necessarily the most parsimonious model. Other less complex models containing these 3-factor interaction terms also were evaluated (Table 2). Five of the 9 possible models had nonsignificant P-values, suggesting each adequately fit the data. Conditional tests among these models indicated that a model containing the terms FCT, CHT, ST, HS, and CS provided the best fit. The biological implication of each term is evaluated below.

Effect of habitat.—Foraging habitat was associated with Osprey sex (HS; discussed below) and with prey size and time (CHT; G² = 54.9, df = 29, P = 0.002) (Table 3). Overall, only 8 of 108 possible interactions between prey size, time, and habitat deviated from random; 3 were

TABLE 2. Summary of statistical models that describe foraging by adult Ospreys from March 1985 to September 1986. See text for descriptions of the factors.

Model	df	G ²	P-value
CST, FCT, CHS, CHT	175	156.2	0.842
CST, FCT, HS, CHT	177	180.8	0.408
CST, FCT, CHS, HT	204	211.0	0.353
ST, FCT, CHS, CHT	209	216.5	0.347
ST, FCT, HS, CS, CHT	211	236.8	0.107
FCT, CHS, CHT	226	924.7	<0.001
CST, FT, FC, CHS, CHT	236	302.4	0.002
ST, FCT, CHS, HT	238	275.7	0.047
ST, FT, FC, CHS, CHT	270	362.8	<0.001

during March–May 1985 and 4 during March–May 1986. During these periods Ospreys exhibited preference for prey in the 10–20-cm and 20–30-cm size range. Note that these periods coincide roughly with yearly increases in the abundance of smaller-size prey (Fig. 1), suggesting that Ospreys were responding to increases in the availability of smaller-size prey.

Examination of the 2-factor tables contained within CHT revealed no significant relationships between foraging habitat and prey size (CH; lambda < 0.127 and P > 0.05 for all size classes), and only 2 of 54 possible time and prey size (CT) interactions were significant. Temporal differences in habitat use (HT), however, were striking (Fig. 2). Male and female Ospreys hunted preferentially in the littoral zone during the brood-rearing and postfledging months (May–August) each year. Negative lambda estimates indicated Ospreys hunted more frequently in the limnetic zone during the non-breeding season (September–April), although use of the limnetic zone during this period was not statistically significant.

Effect of sex.—Choice of prey was independent of Osprey sex (G² = 1.6, df = 2, P = 0.444). Sexes differed, however, in their use of foraging habitat (G² = 42.3, df = 1, P < 0.001), size classes of the available prey (G² = 58.8, df = 2, P < 0.001), and hunting effort over time (G² = 743.5, df = 17, P < 0.001). Males tended to forage in littoral habitat (1,540 of 1,829 observations; hereafter, n = 1,540/1,829) and females in limnetic habitat (n = 679/994). Relative to females, males exhibited preference for the smallest (10–20 cm) prey, while females exhibited preference for 30–40-cm prey (Table 4). Both sexes used prey 20–30-cm long equally and at random.

Temporal differences in capture frequencies

TABLE 3. Summary of captures by adult Ospreys classified by size of prey, time, and habitat. Significance levels for contrasts were calculated by dividing each lambda estimate by its standard error and comparing the value with a normal z-score (Agresti 1984). Counts were weighted by the relative abundance of each size class in each habitat before analysis (see Methods).

Time	10-20 cm			20-30 cm			30-40 cm			Totals
	n ^a	Contrast ^b		n	Contrast		n	Contrast		
		Lambda	SE		Lambda	SE		Lambda	SE	
Mar 1985	44/67	-0.373*	0.150	60/82	-0.005	0.132	2/2	0.378	0.198	106/151
Apr 1985	40/57	-0.694	0.608	55/64	0.086	0.694	2/2	0.609	1.267	97/123
May 1985	73/99	-0.529***	0.141	102/114	0.298*	0.142	2/2	0.232	0.232	177/215
Jun 1985	76/86	— ^c	—	52/60	-0.341	0.210	8/8	0.341	0.546	136/154
Jul 1985	60/66	0.193	0.260	55/62	0.028	0.243	4/5	-0.220	0.721	119/133
Aug 1985	88/89	0.412	0.283	52/57	-0.167	0.242	9/11	-0.245	0.698	149/157
Sep 1985	50/57	0.361	0.235	35/51	-0.386	0.239	1/2	0.025	0.735	86/110
Oct 1985	66/87	0.115	0.253	27/49	-0.407	0.257	2/2	0.292	0.800	95/138
Nov 1985	95/119	0.605**	0.234	43/83	-0.388	0.237	1/2	-0.217	0.783	139/204
Dec 1985	43/62	-0.139	0.205	30/49	-0.305	0.232	1/2	0.444	0.697	74/113
Jan 1986	61/78	1.568	1.065	38/64	0.719	1.065	0/0	-2.287	—	99/142
Feb 1986	58/84	0.081	0.269	50/77	-0.091	0.296	0/1	0.010	0.833	108/162
Mar 1986	44/69	-0.447*	0.197	97/128	0.264	0.248	3/3	0.183	0.668	144/200
Apr 1986	59/80	-0.439*	0.213	100/120	0.410*	0.206	2/3	0.029	0.725	161/203
May 1986	45/63	-1.040**	0.134	113/115	—	—	3/3	1.040	—	161/181
Jun 1986	32/48	—	—	88/106	—	—	3/4	—	—	123/158
Jul 1986	45/54	—	—	67/75	—	—	3/3	—	—	115/132
Aug 1986	55/58	0.327	—	84/90	0.288	0.038	1/2	-0.615	—	140/150
Totals	1,034/1,323			1,154/1,447			47/59			2,235/2,823

^a Number of captures in littoral habitat/total observed in both littoral and limnetic.

^b Ho: Size class of captured prey independent of habitat type in each time period. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

^c Could not be estimated reliably.

also existed between the sexes (Fig. 3). Males hunted relatively more frequently than females before the start of each breeding season (February–March), while females hunted more frequently from June to August. Because results were standardized to sampling effort and number of each sex present, these differences represent actual differences in hunting effort over time.

Effect of time.—In 17 of 18 periods (Table 5) Ospreys exhibited preference for one or more fish and size-class combinations. Among the available fish species, bass generally were captured at random throughout the study (Fig. 4A). Lack of an apparent cycle in bass abundance, and no consistent pattern of preference with respect to time or size class, precluded evaluation of potential lags in preference.

Shad were preferred from September 1985 to February 1986 (Fig. 4B), which coincided with the nonbreeding season in this population of Ospreys. Ospreys hunted preferentially in the limnetic zone during this period (Fig. 2), which suggests preference for shad was associated with a shift in foraging habitat as well. Both 10-20-

cm and 20-30-cm fish were preferred, while fish 30-40 cm in size were largely ignored. Osprey apparently tracked changes in shad abundance closely, lagging less than 0.3 months behind changes in shad abundance (Bulmer's test, see Methods; $r^2 = 0.66$).

Preference for sunfish was evident during May–August 1985 and March–July 1986 (Fig. 4C). These periods coincided with the months of highest sunfish abundance and with the brood-rearing and postfledging periods. As with shad, adults preferentially captured smaller sunfish in the 10-20-cm and 20-30-cm size classes. Sunfish in the 30-40-cm class were underutilized, as indicated by consistently negative lambda estimates. Preference for sunfish lagged 1.2 months (Bulmer's test, $r^2 = 0.78$) behind peak sunfish abundance values, suggesting that Osprey did not respond immediately to changes in sunfish abundance.

DISCUSSION

Shifts in diet choice over time suggest Ospreys switch prey in the manner described by



Fig. 2. Change in relation to time of preferred hunting habitat of adult Ospreys. Histograms with hatching represent statistical preference ($P < 0.05$) for either littoral or limnetic habitat. Vertical lines are standard errors.

Murdoch (1969), Murdoch et al. (1975), and Murdoch and Oaten (1975). Ospreys exhibited distinct preference patterns, shifting from sunfish to shad and back to sunfish. These shifts were strongly tied to concurrent shifts in sunfish abundance, and sunfish were preferred when most abundant. Shad abundance, in contrast, was relatively constant throughout the duration of my study, and shad were preferred by Ospreys only during periods of low sunfish abundance. Shifts from sunfish to shad also coincided with shifts in foraging habitat. Ospreys hunted preferentially in the littoral zone during peak abundances of sunfish and tended to use limnetic habitat when concentrating on shad.

The shift to limnetic habitat suggests some attribute of shad abundance was more favorable in limnetic than littoral habitat. One difference may be potential encounter rates; predators may be more sensitive to prey variance than mean values (Caraco 1980, Real 1980). Although mean absolute abundances of shad were roughly similar in both habitats, variance measures for all three size classes of shad were heterogeneous

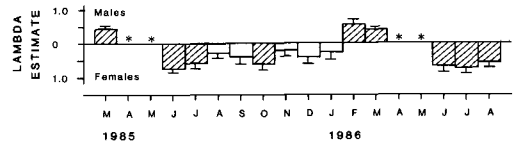


Fig. 3. Change in relation to time of hunting effort by male and female Ospreys. Lambda estimates are standardized to sampling effort and number of each sex present. Hatched areas represent significant differences ($P < 0.05$) in hunting effort. Asterisks denote incubation, when females were not hunting. Vertical lines are standard errors.

over time in littoral habitat. In contrast, variance for 20–30-cm shad, one of the two preferred size classes, was constant over time in limnetic habitat. Consequently, Ospreys may have had higher encounter rates and thus more successful foraging bouts in limnetic habitat. The switch to shad in limnetic habitat after sunfish abundance decreased in littoral habitat also allowed Ospreys to maintain a specialist strategy. Instead of becoming generalists as abundances decreased in the littoral zone, Ospreys remained specialists by switching along habitat lines (see Janetos and Cole 1981).

Strong preference for sunfish was evident from May to August 1985 and March to July 1986. Sunfish preference, however, lagged 1.2 months behind changes in sunfish abundance. Temporal lags in change of preference such as the one exhibited by this population of Ospreys are expected in predators foraging in variable environments, and may be due to delay in the

TABLE 4. Summary of captures by adult Ospreys classified by sex and size class. Significance levels for contrasts were calculated by dividing each lambda estimate by its standard error and comparing the value with a normal z-score (Agresti 1984). Captures were weighted by the relative abundances of each size class before analysis (see Methods).

Size class (cm)	Sex			Contrast ^a	
	Male	Female	Total	Lambda	SE
10–20	911	384	1,295	0.280***	0.044
20–30	893	581	1,474	0.009	0.043
30–40	25	29	54	0.271***	0.074
Total	1,829	994	2,823		

^a Ho: Preference for size class independent of sex. *** = $P < 0.001$.

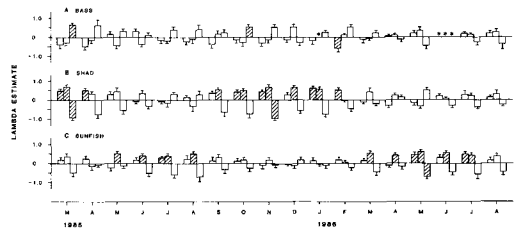


Fig. 4. Change in relation to time of preference for each fish species group and size class by adult Ospreys. Each histogram triplet represents (left to right) 10–20-cm, 20–30-cm, and 30–40-cm fish. Histograms with hatching represent significant preference ($P < 0.05$) or underutilization of a particular fish species group and size class. Vertical lines are standard errors. Asterisks represent lambda estimates that could not be estimated reliably.

TABLE 5. Summary of captures classified by fish species, size class, and time. Significance levels for contrasts were calculated by dividing each lambda estimate by its standard error and comparing the value with a normal z-score (Agresti 1984). Presence of a significant contrast does not indicate where the difference(s) lies; refer to Fig. 5. Counts were weighted by the relative abundance of each fish species and size class before analysis (see Methods).

Time	Sunfish			Bass			Shad			Contrast*	
	10-20	20-30	30-40	10-20	20-30	30-40	10-20	20-30	30-40	Lambda	SE
Mar 1985	13	10	0	8	1	2	42	71	0	-0.839**	0.265
Apr 1985	26	11	0	3	2	2	28	51	0	-0.639*	0.285
May 1985	43	28	2	13	4	0	47	88	0	-0.523*	0.253
Jun 1985	35	44	5	17	0	1	28	19	2	-0.732**	0.290
Jul 1985	35	59	0	11	3	2	21	7	3	-0.601**	0.218
Aug 1985	62	51	1	6	1	1	25	5	9	0.482*	0.235
Sep 1985	24	25	0	8	3	0	25	18	2	0.549*	0.228
Oct 1985	30	21	1	5	0	0	47	28	1	0.691*	0.281
Nov 1985	29	23	0	9	3	1	81	54	2	0.775***	0.229
Dec 1985	14	13	0	4	2	0	54	30	1	0.833**	0.316
Jan 1986	12	15	0	6	2	0	60	59	0	2.230*	1.087
Feb 1986	9	11	0	8	7	0	67	55	0	0.763**	0.297
Mar 1986	17	16	1	9	8	1	38	104	1	0.664***	0.169
Apr 1986	33	42	0	12	9	0	35	65	3	-0.546*	0.275
May 1986	11	53	1	15	13	0	34	49	2	-2.778*	1.139
Jun 1986	20	48	3	9	5	0	24	48	1	-0.435*	0.195
Jul 1986	15	38	2	14	11	1	20	26	0	0.460*	0.233
Aug 1986	23	46	0	15	9	0	20	35	1	-0.354	0.248

* Ho: Prey captured independent of size class in each time period. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

recognition by the predator that previously ignored prey types now constitute profitable food. This recognition may require the formation of new search images that increase the predator's ability to recognize and capture different prey types (Mueller 1971, Pietrewicz and Kamil 1979, McNair 1981). The time required to develop a new search image could explain why Ospreys did not respond immediately to increased sunfish abundance. Thus, rather than the abrupt shift in preference predicted by some foraging models (e.g. "two-armed bandit" model, Krebs et al. 1978; see also Hughes 1979), change in preference could occur gradually.

Whether shifts in preference occur simultaneously with changes in the prey base or exhibit a time lag may depend on whether fish abundances shift gradually or abruptly over time. Strict concordance between Osprey preference patterns and changes in fish abundances was evident for shad (time lag < 0.3 months) but not for sunfish (time lag = 1.2 months). The abundance peaks of sunfish were higher than those for shad (Fig. 1), which suggests that the amplitude of the change affects the time lag. However, the exact relationship between the length of the time lag and the amplitude of the change in abundance is not known and warrants further investigation.

Alternatively, the ability of predators to exhibit strict concordance between preference and abundance may depend on prey periodicity (Craig et al. 1979). The apparent regularity in peaks of fish abundance (sunfish in the spring, shad in the winter) during my 18-month study suggests that fish abundance varies regularly at Newnan's Lake. The apparently equal cycle lengths but different time lags and cycle amplitudes suggest that cycle amplitude rather than periodicity plays the more important role in the establishment of time lags in this population of Ospreys.

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