

TEMPORAL AND SOCIAL ASPECTS OF THE FORAGING
ECOLOGY OF A PISCIVORE, THE OSPREY (Pandion haliaetus)

By

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Abstract of Dissertation Presented to the Graduate School
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(Wildlife and Range Sciences)

I conducted a year-around field study on foraging behavior of a resident population of ospreys (Pandion haliaetus) at Newnan's Lake, Alachua County, Florida, from 1985-1986. I examined (i) foraging behavior of adult ospreys in relation to temporal variation in available prey, and (ii) temporal and social aspects of the ontogeny of foraging. I also monitored dynamics of the fish resource base at the study site.

Adult foraging behavior varied considerably over the 18-month study period. Ospreys preferred sunfish (Lepomis spp.) from March-July each year, but preferred shad (Dorosoma spp.) from September-March. Bass (Micropterus salmoides; Morone saxtilis) were captured in proportion to their abundance. Seasonal shifts from shad to sunfish were strongly associated with increases in sunfish relative and

absolute abundances. Once sunfish abundance declined, ospreys switched back to shad. Relative to sunfish, measures of shad abundance and variability were more constant, suggesting that shad represent a more stable resource base. Time lags between change in prey abundance and shifts between prey types may be due to the inability of ospreys to respond immediately to changes in the prey resource base.

Adults preferentially hunted in the littoral zone of the lake from May-July each year. From August-April, ospreys hunted in pelagic habitat, although preference for pelagic habitat was not statistically significant. Use of littoral habitat was strongly associated with an increase in the abundance and availability of sunfish.

Young ospreys initially captured fish in proportion to their availability by species and size class, ignoring only the larger size class of all fish species. Individual differences in preference patterns existed between unrelated young. Siblings, however, hunted together and had statistically similar prey preference patterns throughout post-fledging. Use of fish resources and foraging mechanics of birds with siblings also approached that of adults at a faster rate than lone birds. Similar resource use and faster rates of learning between siblings suggests post-fledging interactions may facilitate the development of foraging skills.

CHAPTER I

INTRODUCTION AND OVERVIEW

General Background

Diet choice of predators has received considerable attention within the framework of optimal foraging theory. A major disappointment, however, has been the apparent lack of agreement between model predictions and results, and the associated recognition that early foraging models (MacArthur and Pianka 1966, Schoener 1971, 1974, Pulliam 1974, Charnov 1976a, b) may be overly simplistic. To overcome criticisms of simplicity, numerous second generation models that take into account such factors as nutrient requirements (Pulliam 1975), prey-recognition time (Hughes 1979), and prey-handling time (McNair 1981) have been proposed. Unfortunately, tests of the precise quantitative predictions of both first and second generation models often provided only "qualitative" support regarding predictions of diet choice (e.g., Werner and Hall 1974, Emlen and Emlen 1975, Davies 1977, Pulliam 1980, Krebs et al. 1983).

A theme common to most foraging models is that a predator operates within the framework of only a single foraging strategy set. That is, one model is capable of describing most aspects of predator diet

choice. Consequently, deviations in diet choice from those predicted frequently are interpreted as "mistakes" (Jaeger and Barnard 1981) or as "sub-optimal" behavior (see Pyke 1984) in what appears to be an attempt to fit contradictory results to a particular model.

Unfortunately, this perception ignores the possibility that predators might utilize a suite of diet choice algorithms, switching from one to the other in response to changes in the available resource base (Glasser 1982, 1984, Glasser and Price 1982). Such a facultative strategy, where the degree of prey discrimination and choice varies with change in prey abundances, should be advantageous to predators facing highly variable environments. In contrast, predators can concentrate on particular subsets of the available prey base under constant resource conditions. Here, a single model may adequately explain diet choice.

Finally, a key component of foraging behavior and diet choice studies is knowledge about temporal changes in the prey resource base. For instance, a constantly changing resource base requires a high degree of flexibility in predator foraging behavior. One important component of this flexibility is the ability to incorporate information from a changing environment into a new foraging strategy. Therefore, a close coupling of information on prey dynamics with foraging behaviors is needed to fully understand foraging behaviors. Such is the approach I have undertaken here.

Study Organization

My study is organized into two sections comprising three chapters. The first section (Chapter II) is an examination of temporal shifts in prey preference of adult ospreys in relation to prey dynamics. Temporal aspects of foraging (e.g., Doble and Eggers 1978) are an important yet frequently neglected area of predator foraging strategies. For example, predator diet choice may reflect use of nutritionally important prey types prior to the breeding season when mobilization of energy for reproduction is important. Alternatively, diet choice may become increasingly specialized over time as resource abundance increases and predators are able to be selective. This potential for seasonal variation in prey preference often is ignored and can be addressed only by year-around study of the same group of predators.

The second section (Chapters III and IV) concerns the ontogeny of foraging in ospreys. The post-fledging period, when naive young first confront an environment from which they must learn to capture prey, is a crucial time for avian predators. The strongest selective influence on foraging performance likely occurs during this period (Zach and Smith 1981), with learned foraging skills undoubtedly affecting subsequent survival of the young (Kamil 1983). Study of the ontogeny of foraging also has important management implications. Currently, efforts are underway to reintroduce fledgling ospreys to areas from which they have been extirpated. Consequently, identification of factors affecting fledgling survivorship during the post-fledging

period could aid in the development of appropriate management strategies.

Chapter III is an ecological approach to questions regarding the ontogeny of foraging. Here, I examine temporal aspects of the development of prey preference in young ospreys and, in particular, how variability in the prey resource base affects the learning process. Study of how naive young respond to change in their resource base while developing foraging skills could provide insights into foraging behavior not obtainable from study of adults (Kamil 1983).

In Chapter IV I examine behavioral aspects of the development of foraging skills. One hypothesized method by which young increase foraging skills is observational learning (Turner 1964). Here, naive young use experienced conspecifics as role models, learning from others the appropriate cues that lead to successful foraging bouts. One benefit of such social interactions may be an increased rate of learning due to the more frequent exposure to appropriate foraging behaviors. If social interactions lead to increased rates of learning, managers may wish to modify reintroduction procedures to realize the benefits associated with sociality. Together, Chapters III and IV provide an ecological and behavioral perspective of the ontogeny of foraging behaviors.

CHAPTER II

TEMPORAL CHANGE IN PATTERNS OF PREY PREFERENCE IN OSPREYS

Introduction

Suggestions that predators forage in an optimal manner first were articulated by Emlen (1966) and MacArthur and Pianka (1966), who each developed explicit mathematical models predicting how predators should forage under certain circumstances. The basic premise underlying these and subsequent models on foraging behavior and diet choice is that optimal foraging, as contrasted with random foraging, maximizes Darwinian fitness (see reviews by Schoener 1971, Pyke et al. 1977, Pyke 1984).

One criticism of diet choice models is the rapidity with which both the quantitative and qualitative predictions break down when models are modified in a realistic manner. For instance, models based solely on energetic requirements (MacArthur and Pianka 1966, Schoener 1971, Pulliam 1974, Werner and Hall 1974, Charnov 1976a) predict that partial consumption of lower-ranked prey should not occur, yet contradictory (e.g., Willson 1971, Goss-Custard 1977) as well as supportive results (e.g., Smith and Follmer 1972, Zach and Falls 1978) are common in the literature. Furthermore, the lack of mutually

exclusive predictions often makes it difficult to determine which model best describes predator diet choice.

Unfortunately, many foraging studies also have concentrated on foraging behaviors only during discrete time periods (e.g., non-breeding season, Craig 1978; winter versus summer, Baker and Baker 1973, Opdam 1975). One consequence of this approach is the potential loss of information on temporal aspects of foraging; in particular, how diet choice at time t is affected by prey and predator dynamics at time $t-1$. For example, temporal variation in prey preference may result from both changes in prey abundance and particular stages in predator life histories. Preference for a particular prey type may be strong when prey abundances are high and predators have the option to be "choosey," but less strong as abundances decline and predators are forced to consider alternate prey. Another example may be the need for "nutrient-rich" prey (e.g., Pulliam 1975, Westoby 1974, 1978) prior to the breeding season. Once the breeding season finishes, preference for nutrient-rich prey may decrease. In both instances, failure to recognize the relationships among study period, prey abundances and predator life histories makes interpretation of results difficult. Moreover, relationships such as these would be apparent only by year-around study of the same population of predators.

Here I examine the influence of a variable resource base on patterns of prey preference in a resident population of ospreys (Pandion haliaetus) in north-central Florida. Ospreys are ideal study organisms for examining temporal relationships and prey preference because of their high visibility and lack of susceptibility to certain

external constraints (e.g., predation, Martindale 1982) that often modify foraging behaviors. Moreover, ospreys are obligate piscivores and consume a resource amenable to sampling. Consequently, prey dynamics are relatively easy to monitor.

Several objectives were accomplished by my research. First, I examined the effect of change in the underlying prey resource base on patterns of prey preference in ospreys. In general, a predator's foraging strategy, and hence its diet, depends on whether it occupies an environment where the prey base is constant or variable over time (Schoener 1971, 1974, Pulliam 1974). Under constant resource conditions, predators should exhibit either an obligate specialist or obligate generalist strategy. If prey abundance is consistently low, a generalist strategy should prevail, while a specialist strategy is advantageous if prey abundance is relatively high and constant.

A facultative strategy, the implicit strategy of most optimal foraging models, should be used in environments where the prey base is highly variable. Under variable resource conditions, prey preference patterns of ospreys should indicate a switch from a generalist to specialist strategy as fish abundance increases. Measures of preference at low fish abundance levels should indicate use in relation to availability (i.e., "random" use), while preference should be independent of frequency at relatively high abundance levels. Thus, a major goal of my research was to determine the extent to which ospreys switch from a generalist to specialist foraging strategy as fish abundances varied over time.

Second, I wished to examine the possible role of time lags in response by ospreys to changes in prey availability. Because an important component of foraging models is information on prey availability, it has been argued that predators should continuously sample from the environment as insurance against future change (Smith and Sweatman 1974, Oster and Heinrich 1976). Once abundances change and use of a particular prey type is no longer profitable, predators should switch emphasis and concentrate on the particular prey type currently profitable (Murdoch 1969, 1973, Murdoch and Oaten 1975).

Whether shifts in preference patterns of ospreys occur simultaneously with change in the fish resource base, or exhibit a time lag, may depend on whether fish abundances shift gradually or abruptly over time. Abrupt shifts in abundance that force ospreys to switch preference undoubtedly introduce a time lag, while gradual shifts in abundance should allow ospreys to simultaneously shift preference. Consequently, examination of the possible role of time lags requires close coupling of the dynamics of the fish resource base with osprey foraging behavior.

Methods

Study Area

My research was conducted on Newnan's Lake, Alachua County, Florida, from March 1985-September 1986. Newnan's Lake, located 15 km east of Gainesville, Florida, is a shallow (<3 m depth), 2400 ha hyper-eutrophic lake (Shannon and Brezonik 1972) rimmed with

baldcypress (Taxodium distichum) and mixed hardwoods. Most of Newnan's Lake is open water, although from May-October much of the lake periphery is covered by hydrilla (Hydrilla verticillata), coontail (Ceratophyllum spp.), and spatterdock (Nuphar luteum) vegetation.

Changes in the lake vegetation structure are due primarily to fluctuation in water level, which varies from a 3 m depth in winter months to a 1.5 m depth in summer. This variation in water depth creates different lake habitats at different times of the year. During winter months, when the lake is deepest, the lake is relatively open and vegetation is absent. From May-October, however, decreased water depth allows vegetation to establish roots in the underlying lake substrate and cover up to 10% of the lake surface area. The creation of two lake habitats during this period, a littoral and pelagic zone, affects the underlying fish resource base and presents ospreys with two different foraging habitats.

Evaluation of Prey Base

I used electrofishing to estimate the fish resource base available to ospreys (see review by Reynolds 1983). This technique uses an electrical charge to stun fish for capture and subsequent measurement or determination of desired parameters, and is considered an effective method by which abundances can be estimated. One advantage of electrofishing from the standpoint of this study is that it samples fish at the top of the water column. Fish thus sampled represent what is available to ospreys, who cannot dive to great depths to capture prey. While electrofishing efficiency is known to be size related

(Sullivan 1956, Reynolds and Simpson 1978) and hence biased against small fish ("fingerlings," <5 cm), estimates of length frequencies of larger fish are considered reasonably accurate (Reynolds 1983). Because ospreys at Newnan's Lake typically caught fish in excess of 10 cm (Collopy 1985, this study), I did not consider this bias against fingerlings to be a disadvantage.

Fish availability was estimated monthly throughout the 18-month study period. I ran 12 15-min electrofishing transects, six each in the littoral and pelagic zones, on two consecutive days. Capture results were used to estimate the relative abundance of each fish species. Trends in absolute abundance were based on the number captured per 15-min transect. Fish parameters collected included fish species, weight (g), and total length (cm). I excluded from analysis unlikely prey for ospreys (e.g., bottom-dwelling brown bullhead, Ictalurus nebulosus) because I felt their inclusion would bias results by inflating preference measures for other prey types.

Osprey Foraging Behavior

I observed osprey foraging behavior from a boat anchored offshore at locations that facilitated simultaneous observations on several birds. Individual ospreys were chosen at random and 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 due to difficulties associated with maintaining observation of the same individual, and because it increased the number

of independent samples. Distinction between sexes were made 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. Every effort was made to ensure continuity in the sampling scheme, although inclement weather and logistical problems frequently forced minor adjustments in the sampling design.

Identification of prey species captured was relatively straightforward owing to distinctive fish silhouettes and the anterior-posterior manner in which ospreys carried fish to minimize wind resistance. I assigned prey captured to one of three 10 cm size classes (10-20 cm, 20-30 cm, 30-40 cm) based on relative length of the fish to the bird (see Poole 1982). The approximate location and lake habitat type of each capture was noted on 7.5 min USGS topographic maps of the lake.

Analysis

I used log-linear analysis to develop statistical models best describing use of the available fish resource base over time by ospreys. Log-linear analysis is a procedure similar to analysis-of-variance for use on multidimensional categorical data (e.g., habitat type, prey size class) (Bishop et al. 1975, Feinberg 1980, Agresti 1984). The procedure examines models composed of all factors and their interactions in a hierarchical fashion; that is, whenever models containing higher order interactions are considered, lower order effects composed of the same factors also must be included

in the model. The presence of significant interactions between factors of any model suggests that that particular model does not fit the data. Non-significant interactions for any combination of factors suggests each factor is independent and, therefore, represents a model that fits the data.

Hereafter, factor refers to the variables of interest, level to categories within each factor, and cell to the intersection of >2 levels. Factors analyzed included prey type, prey size class, time (month), habitat (littoral or pelagic), and osprey sex.

Model cells representing prey captured by each individual osprey were weighted by the relative abundance of each fish species and size class prior to 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, respectively, should not have identical (i.e., 0.5) expected capture probabilities if ospreys are foraging 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).

Standardized lambda estimates were calculated for each cell in the model. Basically, lambda estimates are a measure of the difference between expected and observed values (i.e., standardized cell residuals) that can be used as a measure of preference for a particular fish species and size class. Lambda estimates have an asymptotic standard normal distribution and can be compared to normal z-scores for significance testing. Here, I considered significant positive lambda estimates to indicate "preference" for a particular fish resource type.

Non-significant 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).

I first evaluated all possible models using the likelihood ratio statistic, G^2 , eliminating those with significant P -values. When several 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 any 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 cell lambda estimates as described above.

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

Results

Prey Base

Fish data were collapsed into three categories representing bass (largemouth bass, Micropterus salmoides; striped bass Morone saxtilis), sunfish (warmouth, Lepomis gulosus; bluegill, L. macrochirus; redear sunfish, L. microlophus), and shad (gizzard shad, Dorosoma cepedianum);

threadfin shad, D. petenense). Prey species were categorized for several reasons. First, the fish species placed together are behaviorally and ecologically similar. For instance, all three sunfish interbreed (Breder and Rosen 1966:439-440, Childers 1967), as do both species of shad (Minckley and Krumholz 1960). Second, food and foraging habits of the categorized species are similar (references in Breder and Rosen 1966, Carlander 1969, 1977). Last, and most important, body forms of grouped fish species are similar, and it is unlikely that ospreys are capable of distinguishing minute differences (e.g., presence of red dot on lateral surface of redear sunfish) between species in the absence of gross behavioral differences.

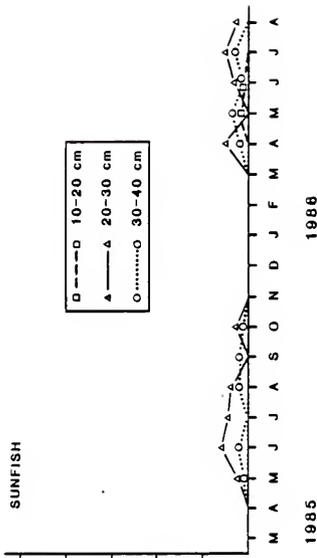
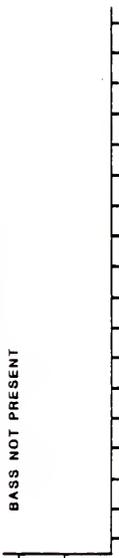
Prey relative abundance. Prey relative abundances varied across species groups, size classes, and time. Major differences existed primarily between lake habitats, with bass not present in the pelagic zone and sunfish found there only seasonally. Furthermore, overall abundance of all fish species groups was higher in the littoral than in the pelagic zone.

Bass were not found in the pelagic zone (Fig. 2-1). In the littoral zone, abundance was fairly constant within each size class, but no temporal pattern of change was obvious. Not unexpectedly, differences in availability among bass size classes reflect size class rankings, with each smaller size class more prevalent than its next larger size class.

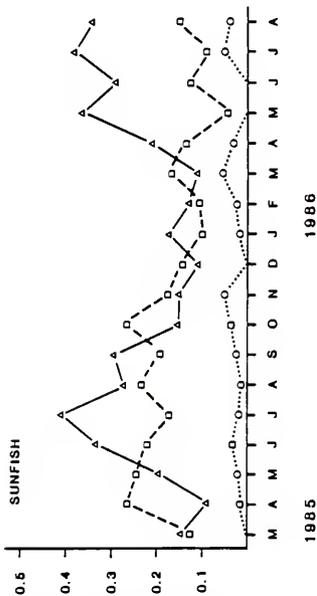
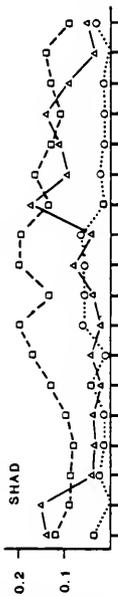
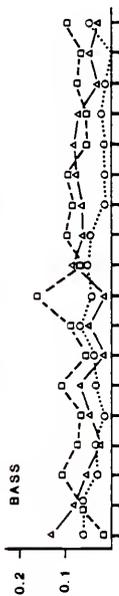
Shad were found in approximately the same proportion in pelagic and littoral habitats (Fig. 2-1). A major difference, however, was the shift in the most common size class between lake habitats. Smaller

Figure 2-1. Relative abundance of each fish species group in littoral and pelagic habitat.

HABITAT TYPE: PELAGIC



HABITAT TYPE: LITTORAL



PROPORTION OF EACH FISH SPECIES AND SIZE CLASS

1988

1985

1986

1985

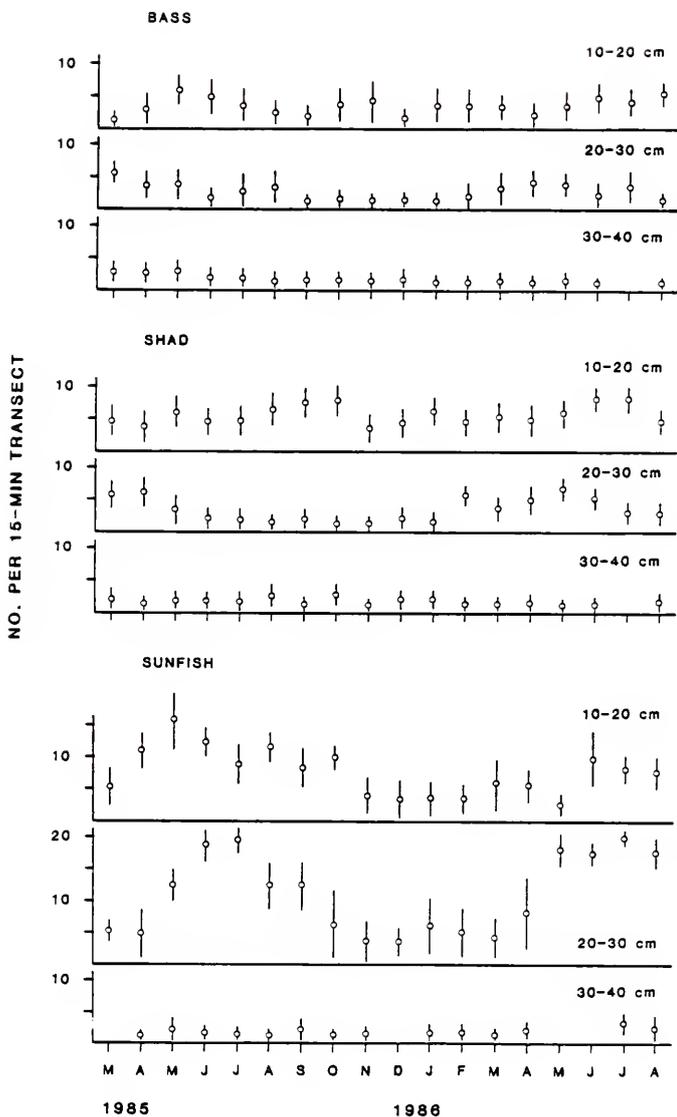
shad (10-20 cm) were more prevalent in the littoral zone, while 20-30 cm sized shad were more common in pelagic habitat. This difference probably reflects the tendency of smaller-sized individuals to remain in shallower waters until they are sufficiently large to survive and compete in deeper waters. The numbers of shad in the 30-40 cm range were consistently low in both lake habitats. Unlike bass, the shad population appeared to cycle, with high and low abundances occurring in the winter and summer months, respectively.

Sunfish exhibited patterns different from bass and shad. They were present year-around in the littoral zone but only seasonally in the pelagic zone (Fig. 2-1). In the littoral habitat, 20-30 cm sized sunfish exhibited a cyclic pattern, peaking between May and August. No such obvious pattern was apparent for 10-20 cm size class, although there appeared to be a general decrease in abundance in this size class throughout the study period. Whether this represents a longer cycle is not known. Sunfish 30-40 cm long were fairly constant in abundance but represented a small proportion of the available fish overall. Sunfish also exhibited two brief, distinct movements into the pelagic zone.

Prey absolute abundance. Patterns of change in absolute abundance were, in general, similar to those exhibited for relative abundance. Estimates of relative and absolute abundance of bass revealed no apparent differences for any of the three size classes (Fig. 2-2). Similarly, patterns of absolute abundance for shad in littoral habitat were similar to those of relative abundance. In the pelagic zone, however, patterns of absolute abundance of 10-20 cm and 20-30 cm sized shad differed from relative abundance (Fig. 2-3). Instead of

Figure 2-2. Mean number (± 1 SD) per 15-min sample transect ($n = 6$) of each fish species group and size class in littoral habitat.

HABITAT TYPE: LITTORAL



fluctuating, numbers of shad in these two size classes were fairly constant over time. Numbers of shad in the pelagic zone also were more constant than numbers in the littoral zone. Patterns of change in absolute abundance of sunfish were similar to those of relative abundance in both littoral (Fig. 2-2) and pelagic (Fig. 2-3) habitats.

Distinct cycles in fish numbers in both lake habitat types, and when habitats are combined, are apparent when estimates of absolute abundance are summed across prey groups and size classes (Fig. 2-4). In general, fluctuations in prey absolute abundance were greater in the littoral than in the pelagic zone. Thus, the pelagic zone represented a more constant habitat with respect to prey numbers than did the littoral zone.

Prey patchiness. Variation or "patchiness" in distribution of each fish species and size class is shown in Figures 2-2 and 2-3. To determine whether variation was constant through time for each fish group and size class, Bartlett's test for homogeneity (Sokal and Rohlf 1981:403-412) was applied to the monthly electrofishing sample variances. With the exception of 30-40 cm sized shad ($\text{Chi-square} = 18.21$, $\text{df} = 17$, $\underline{p} > 0.05$), all fish species groups and size class combinations in the littoral habitat exhibited significant differences in variance over time ($\text{Chi-square} > 32.53$ for each combination, $\text{df} = 17$, $\underline{p} < 0.05$). In contrast, variances in 10-20 cm and 20-30 cm sized shad in the pelagic zone were constant over time ($\text{Chi-square} < 22.67$ for each size class, $\text{df} = 17$, $\underline{p} > 0.05$). Samples for sunfish and for 30-40 cm sized shad were not sufficiently continuous for comparison of variances.

Figure 2-3. Mean number (± 1 SD) per 15-min sample transect ($n = 6$) of each fish species group and size class in pelagic habitat. Bass were not present in pelagic habitat.

HABITAT TYPE: PELAGIC

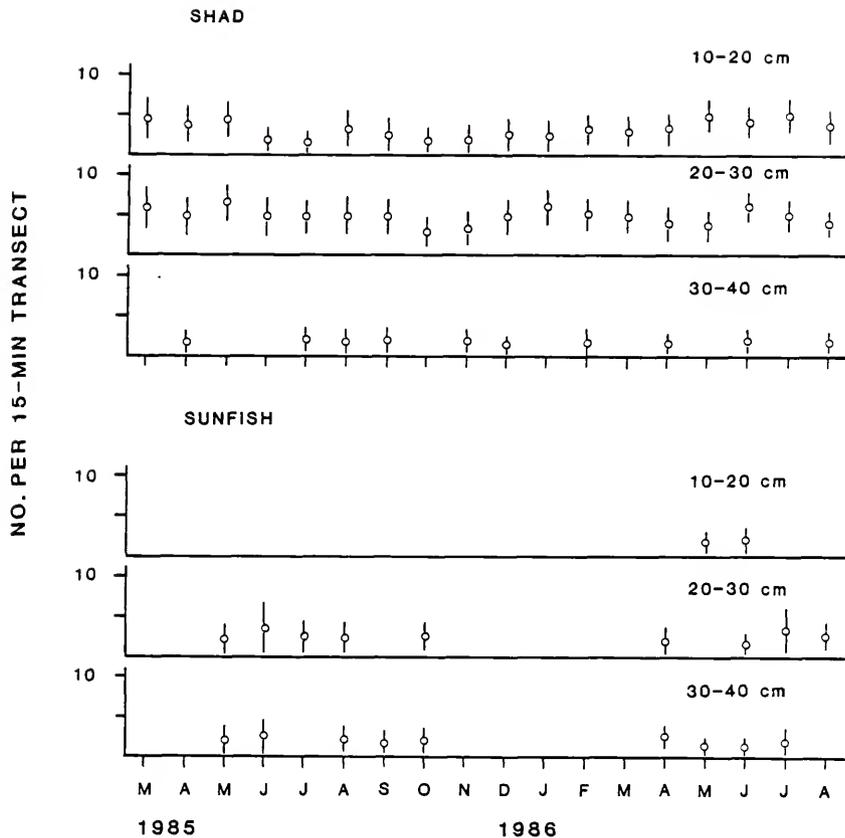
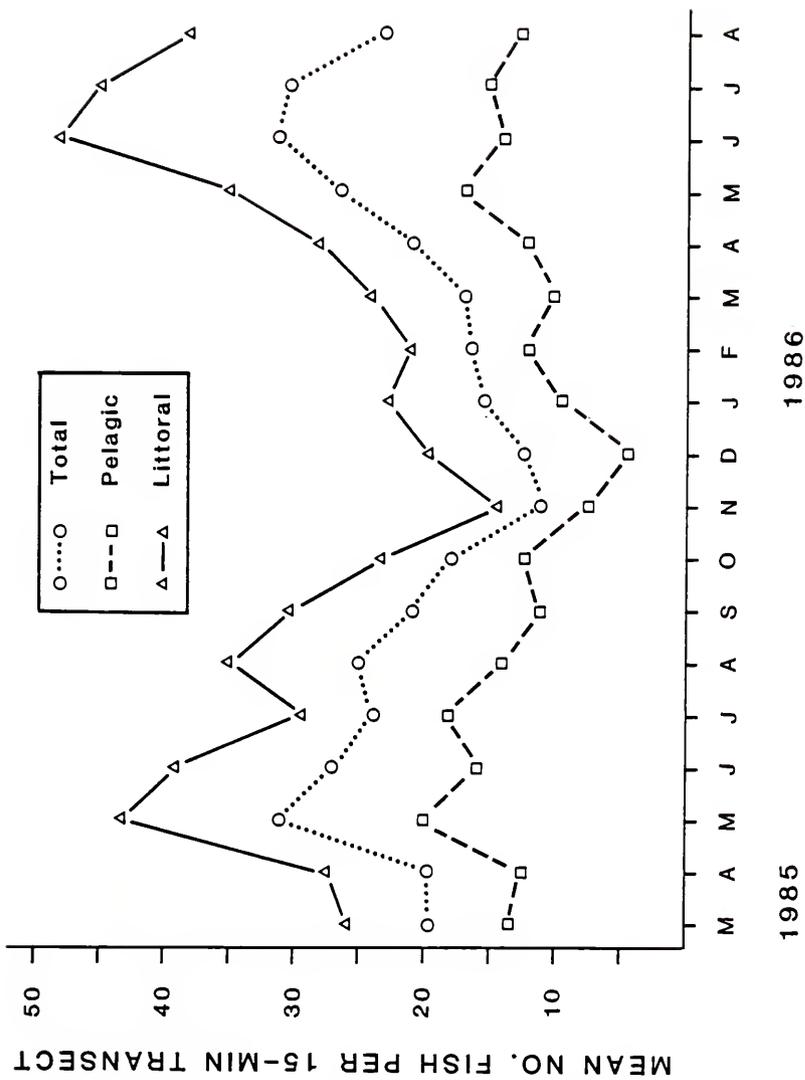


Figure 2-4. Mean number of fish captured per 15-min sample transect ($n = 6$) in littoral and pelagic habitat, and both habitats combined. Data are summed across all fish species groups and size classes.



One problem with the use of Bartlett's test as a measure of heterogeneity in variance of each fish group and size class over time is its sensitivity to non-normal distributions. Because the underlying distribution of the fish groups more closely follows a Poisson than a normal distribution, these differences may reflect non-normality of data rather than differences in variances. Nonetheless, use of Bartlett's test here provides some idea whether variation in the abundance of each fish group and size class is constant or variable over time.

In general, differences in prey abundances between lake habitat types presents ospreys with two different foraging environments. Prey from all three fish groups were present year-round in the littoral zone, although abundances varied. In contrast, bass were not found in pelagic habitat and sunfish were found there only seasonally. Shad were found in both lake habitats, but were more variable in the littoral than in the pelagic zone.

Adult Foraging Patterns

A total of 2823 successful captures (roughly 15 per observation day) were observed over the 18-month study period. Because of small sample sizes relative to the number of classifying variables, I was forced to collapse data from each observation day into monthly periods centered about each electrofishing sample. Collapsing daily data into monthly periods also was required to prevent generation of cell expected values less than 1.0.

Several factors also forced me to combine individual foraging data and examine foraging behavior at a population rather than individual level. First, I was unable to capture and color-mark adults. Instead, I determined the identity of particular birds by observing their return to individual nesting trees and, occasionally, their unique plumage characteristics. While this allowed for identification of individuals during the breeding season, its accuracy as a means of identification during the non-breeding season is not known.

Preliminary analysis of data on individually recognized birds (roughly 35% of the entire data set) revealed some differences among individuals. In general, however, these differences were caused by <3 of the 21 known birds. The remaining birds were similar statistically. I therefore concluded that my collection and analysis of data at a population level adequately represented individual foraging behaviors. Even though Chesson (1984) suggests foraging data must ultimately be analyzed at the individual level, my analysis of data at a population level should, at worst, widen confidence intervals about my measures of preference. Second, as described above, I had to combine data to avoid generating expected cell values less than 1.0.

Best-fit Model

Tests of partial and marginal associations were used to determine which factors and interactions were necessary in the first-pass models. Non-significant partial and marginal associations suggests a particular interaction between two factors is not needed in the model. Interactions having both significant partial and marginal associations

are considered necessary, while those having only one significant association are considered questionable (Brown 1976).

Hereafter, shorthand notation will be used to describe the relationships among the factors, where F represents the available fish species groups, C the fish size classes, S osprey sex, H the lake habitat type, and I the time interval. For example, the term FCT means that prey types, size class, and time have statistically significant associations with one another. Biologically, the term states that use of the available fish species groups and size classes varied over time.

Tests of partial and marginal associations revealed that no four-factor interactions had significant marginal or partial associations. Consequently, all four-factor terms were excluded from consideration. Four of 10 possible three-factor interactions had significant partial and marginal associations, while 3 of 10 had either a significant partial or marginal association (Table 2-1). All two-factor interaction terms had at least one significant test. Because of the high number of possible models and their complexity, I decided to consider only those terms having both significant partial and marginal associations. Terms retained for possible models included FCT, CHS, CHT, and CST. Because of the hierarchial nature of log-linear models, all possible two-factor terms with significant partial and marginal associations were contained within the three-factor terms and were automatically considered.

The model FCT,CHS,CHT,CST represents the most complex, but not necessarily the most parsimonious, model. Other models less complex, but containing the necessary significant interaction terms, also were

Table 2-1. Tests of partial and marginal associations for the model factors prey type (F), prey size class (C), habitat (H), osprey sex (S), and time (T). No four-factor interaction terms had significant partial or marginal associations and were not considered.

Effect	Partial Association			Marginal Association		
	df	G ²	P-value	df	G ²	P-value
Two-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
Three-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 ^a	146.7	<0.001	61 ^a	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 a negative df. See methods.

evaluated (Table 2-2). Five of the 9 possible models had non-significant P-values, suggesting each of these models adequately fit the data. Conditional tests among these models revealed that ST,FCT,HS,CS,CHT provided the best fit. This model states that prey choice among adult ospreys varied simultaneously with prey size class and time (FCT), that size classes used varied simultaneously over habitat type and time (CHT), and that differences between the sexes existed over time, between habitat types, and among prey size classes (ST, HS, and CS, respectively). In general, the model terms represent differences in prey use over time, between sexes, and between habitat type. Each set of differences will be considered individually.

Effect of habitat. Foraging habitat was strongly associated with osprey sex (HS, see below), and with prey size class and time (CHT). The term CHT states that temporal differences in use of the prey size classes existed independent of prey type, and that they were related to habitat. To properly interpret CHT requires that each term be evaluated in light of the other two terms.

Examination of CH revealed no relationship between foraging habitat and each prey size class ($\lambda < 0.127$ and $P > 0.05$ for all three size classes). This suggests the association between CHT is due primarily to interactions between CT and HT. Examination of λ estimates for CT revealed no apparent patterns. Only 2 of 54 possible time and prey size class interactions deviated from random, suggesting these values represent possible outliers that overly influenced the G^2 statistic for this term.

Table 2-2. Summary of possible models describing foraging by adult ospreys in 1985-86. Factors not separated by commas are associated with one another and should be interpreted as described in text.

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

Temporal differences in use of habitat, however, were very apparent (Fig. 2-5). Ospreys hunted preferentially in the littoral zone during the brood-rearing and post-fledging months each year. Negative lambda estimates indicate ospreys hunted more frequently in the pelagic zone during the non-breeding season (August-April), but its use was not statistically significant.

Effect of sex. Lack of an interaction between sex and prey types means that preference for particular prey types was constant between sexes. Instead, differences between sexes were associated with habitat, prey size classes, and time.

Sexual differences in preferred foraging habitat were pronounced and constant over time. Males tended to forage in the littoral zone while females exhibited preferential use of the pelagic habitat ($\lambda = 0.186$, $SE = 0.027$, $P < 0.001$).

Differences also were apparent in the use of the fish size classes. Males exhibited preference for the 10-20 cm size class ($\lambda = 0.280$, $SE = 0.044$, $P < 0.001$) while ignoring the 30-40 cm size class ($\lambda = -0.271$, $SE = 0.074$, $P < 0.001$). Females exhibited the opposite pattern, concentrating on prey in the 30-40 cm size class and ignoring 10-20 cm sized prey types. Neither sex exhibited preference for 20-30 cm sized prey, using prey of this size class equally and at random ($\lambda = 0.009$, $SE = 0.043$, $P > 0.05$). These differences were constant across all fish species groups and time.

Temporal differences in capture frequencies also existed between the sexes (Fig. 2-6). Males hunted relatively more frequently than females prior to the start of each breeding season (February-March)

Figure 2-5. Change in relation to time of preferred hunting habitat of adult ospreys. Histograms with crosshatching represent statistical preference ($P < 0.05$) for either littoral or pelagic habitat. Vertical lines are standard errors.

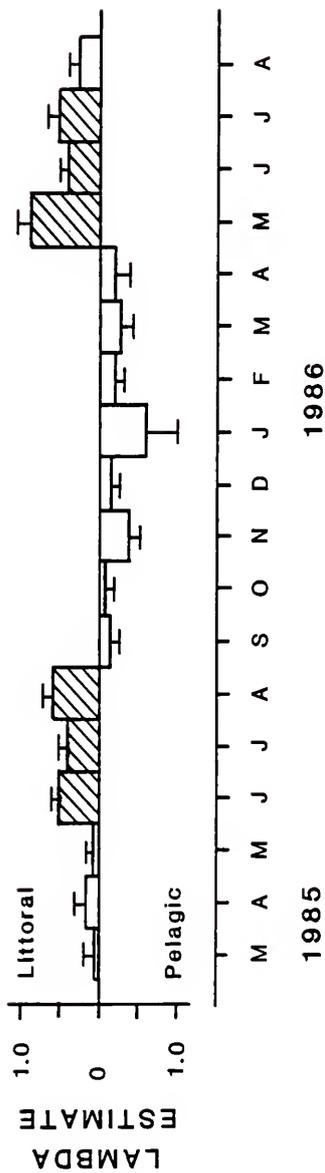
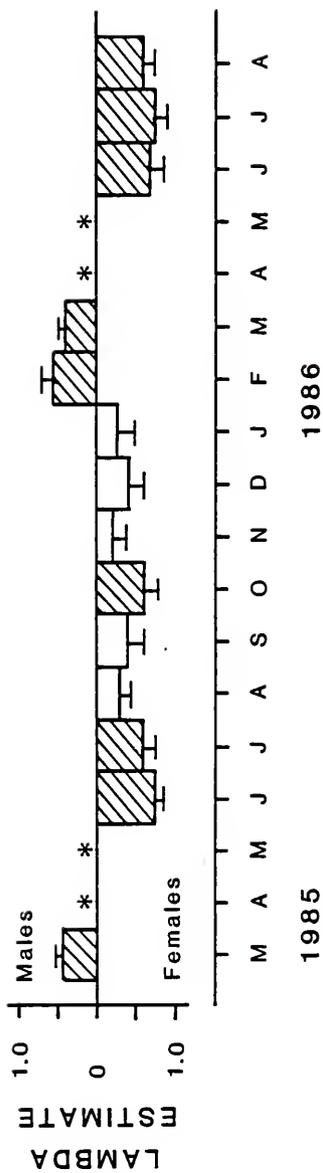


Figure 2-6. Change in relation to time of hunting effort by male and female ospreys. Lambda estimates are standardized to sampling effort and number of each sex present. Cross-hatched areas represent significant differences ($P < 0.05$) in hunting effort. Asterisks denote incubation, when females were not hunting. Vertical lines are standard errors.



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 true differences in hunting effort over time.

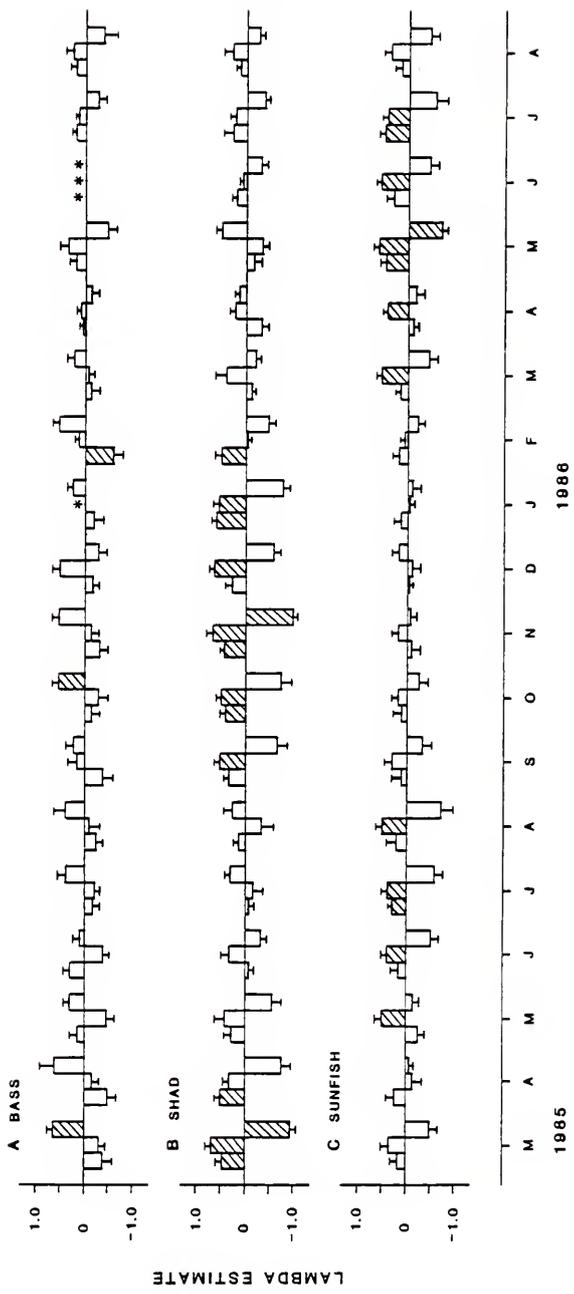
Effect of time. Use of the available fish species groups and size classes was strongly affected by time (Fig. 2-7). Sexes did not differ in their use of the available fish species groups, nor was there an association between habitat and use of prey. Ospreys did not exhibit consistent preference for bass, essentially capturing bass at random (Fig. 2-7a).

With few exceptions, preference for shad occurred during the non-breeding season (Fig. 2-7b). During this period, osprey exhibited statistical preference for shad in the 20-30 cm size class. Unlike in sunfish, however, no one size class was consistently under-utilized. Instead, there existed positive, non-significant preferences for all size classes over time.

Use of sunfish exhibited a cyclic pattern over the 18-month study period (Fig. 2-7c). Peaks occurred in May-August 1985 and in March-July 1986. Examination of the 8 time periods when statistical preference was expressed revealed that adults preferentially concentrated on sunfish in the 20-30 cm size class. In two of the periods they also exhibited preference for 10-20 cm sized sunfish. Sunfish in the 30-40 cm size class were consistently under-utilized, although none of the lambda estimates was statistically significant.

Figure 2-7.

Change in relation to time of preference for each fish species group (A = bass, B = shad, C = sunfish) and size class by adult ospreys. Each histogram triplet represents, left to right, 10-20 cm, 20-30 cm, and 30-40 cm sized fish. Histograms with cross-hatching represent significant preference ($P < 0.05$) or under-utilization of a particular fish species group and size class. Vertical lines are standard errors. Asterisks represent lambda estimates that could not be estimated reliably.



Discussion

Shifts in diet choice over time suggest ospreys are switching prey in the manner described by Murdoch (1969) and Murdoch and Oaten (1975). Ospreys exhibited distinct patterns of preference, shifting preference from sunfish to shad then back to sunfish. These shifts were strongly related to concurrent shifts in sunfish abundance, with preference for sunfish exhibited during the period they were most abundant. Shad, in contrast, were relatively constant throughout the duration of my study. Ospreys exhibited preference for shad only during periods of low abundance of sunfish.

Associated with the shift from sunfish to shad was a shift in foraging habitat. Ospreys preferentially hunted in the littoral zone during peak abundances of sunfish and tended to use pelagic habitat when concentrating on shad. It is important, then, to distinguish between prey switching between habitats and within habitats. The former is considered a consequence of predator aggregation (Krebs et al. 1983), while the latter is a response to changes in the proportions of available prey. The switch between foraging habitats documented here raises several questions. First, why did ospreys switch to pelagic habitat to forage on shad rather than continue to forage in the littoral zone, particularly since shad were present in littoral habitat?

Switching between different prey types in different habitats is considered a function of both predator and prey densities (Royama 1970, Murdoch et al. 1975). Predators should be expected to switch foraging

habitat when profitability decreases. The applicability of aggregation to switching behavior exhibited by ospreys is, however, questionable. Osprey numbers were not increasing in the time periods before the habitat switch, nor is it likely osprey foraging had a significant impact on the fish resource base. Rather, the switch to pelagic habitat and use of shad appears primarily related to decreases in the abundance of sunfish in littoral habitat.

A second question revolves around attributes of shad abundance that encouraged the switch from littoral to pelagic habitat. Within habitats, predators are thought to be sensitive to change in prey absolute abundance (e.g., Hughes 1979). If so, then ospreys should have switched to shad in the littoral zone since their absolute abundance was increasing as sunfish decreased in abundance. Instead, the shift to pelagic habitat suggests some attribute of shad abundance was more favorable in the pelagic zone. One difference may be potential encounter rates. Several authors have suggested predators may be more sensitive to prey variance than mean values (e.g., Caraco 1980, Real 1980). Although mean absolute abundances of shad were roughly similar in both habitats, variance measures were higher in littoral than in pelagic habitat. Consequently, ospreys may have had higher encounter rates and thus more successful foraging bouts in pelagic habitat.

Instead of shifting only along a single continuum represented by prey, shifts also could occur along a second continuum incorporating habitat differences. Switches along habitat lines most likely would be a function of the frequency and magnitude of change in the respective

prey resource bases (Janetos and Cole 1981). For example, the switch to pelagic habitat by ospreys after sunfish abundance decreased could represent a shift from a specialist strategy in littoral habitat to one in pelagic habitat. Based on the patterns shown here, shad in pelagic habitat represent a relatively constant resource base. Ospreys switched to littoral habitat when the abundance of sunfish increased to a point where numbers alone made their capture advantageous. Thus, rather than shifting to a more generalist strategy, predators may remain specialists by switching to alternate habitats provided these habitats contain high prey abundances.

Preference patterns for the three prey types suggested ospreys were specialists when overall fish abundance was high and fairly general in diet choice when abundance was low. From May-September 1985 and June-August 1986 ospreys preferentially captured sunfish in the 10-20 and 20-30 cm size classes. Preference for sunfish, however, did not develop until overall prey abundance peaked. Moreover, continued preference for sunfish even when overall abundance was decreasing suggests there existed a time lag from when fish abundances changed until ospreys modified their diet. Instead of responding immediately to change in sunfish abundance, ospreys continued to use sunfish for a short time period.

Temporal lags in change of preference such as the one exhibited by this population of ospreys are likely in predators foraging in variable environments, and may be due to delay in the 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). Consequently, predators may continue to capture less profitable prey types until a new search image is formed. Similarly, the time required to develop a new search image could explain why ospreys did not immediately respond to increases in the abundance of sunfish. Instead, change in preference was gradual. 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. Lag in preference could simply reflect the time required to develop a new set of search images appropriate for a different resource base.

New search images probably develop during "intermediate" periods of prey abundance, during which time prey preference should be frequency dependent (Murdoch 1969, Fullick and Greenwood 1979, but see Horsley et al. 1979). Here, if absolute abundances are summed across both habitat types, the most abundant fish species group during these "intermediate" periods is shad. Unfortunately, similarity in fish absolute and relative abundance patterns makes it difficult to determine whether preference patterns of osprey were frequency dependent or proportional to availability. In general, however, osprey preference patterns indicated a switch from preference for a subset of the available prey (sunfish) to generality in diet.

Strict concordance between osprey preference patterns and fish abundances seems unlikely unless changes in abundance are gradual. Although the duration of my study was only 18 months, the apparent

regularity in peaks of fish abundance suggests that fish abundance cycles regularly at Newnan's Lake. Whether the length of a time lag is a function of cycle length in prey is not known. The ability of facultative foragers to exhibit strict concordance between preference and abundance may depend on the periodicity of prey (e.g., Craig et al. 1979). Gradual change would allow sufficient opportunity for predators regularly to sample and respond to change. In contrast, rapid change in abundance increases the potential for introduction of a time lag in change of osprey preference patterns.

CHAPTER III

THE ONTOGENY OF PREY PREFERENCE: EFFECT OF A VARIABLE RESOURCE BASE

Introduction

Avian foraging studies tend to ignore the post-fledging period during which foraging skills are developed by young, and instead concentrate on behavior exhibited by adults. The strongest selective influence on foraging performance, however, may occur during the post-fledging period (Zach and Smith 1981). Skills learned during this period undoubtedly affect survival of the young and may influence foraging performance as an adult (Kamil 1983).

Improvement in foraging skills over time has been demonstrated for a variety of bird species, including brown pelicans, Pelecanus occidentalis (Orians 1969), starlings, Sturnus vulgaris (Stevens 1985), herring gulls, Larus argentatus (Verbeek 1977), glaucous-winged gulls, L. glaucescens (Searcy 1978), and royal terns, Sterna maxima (Buckley and Buckley 1974). Missing from many of these studies, however, is knowledge of the prey dynamics during the period young are first sampling from an environment unfamiliar to them. Variability in the environment undoubtedly affects the learning process in young birds, and information on the dynamics of the prey base during this learning period is required to understand fully how foraging skills are developed.

Here I examine the ontogeny of foraging in ospreys (Pandion haliaetus), exploring the relationship between development of foraging skills and dynamics of the fish resource base. First, I wished to determine how prey dynamics during the post-fledging period affected temporal aspects of the ontogeny of foraging. For example, does preference for particular prey types develop at faster rates if the prey resource base is relatively stable? Or, in contrast, does a highly variable environment extend the learning period by making it difficult for naive young to determine which cues are most relevant to foraging decisions? In addition, I wished to compare young from different years to determine whether foraging skills develop in a similar fashion if the temporal sequence of variation in the fish resource differs between years. Specifically, is a model that adequately explains the ontogeny of foraging in one year applicable in the next?

Second, I characterized use of the available fish resources by young birds, examining how use of available prey resources varied in response both to fluctuation in fish availability and to the continuously improving skills of young. This implies a two-factor interaction affecting learning. As a bird improves its foraging skills, perhaps learning to concentrate on a particular prey type, the availability of that resource may suddenly change. Cues that previously led to successful foraging bouts may no longer be relevant. Lastly, as an indicator of how young forage, I compared their use of resources with adults who simultaneously are sampling from the same resource base.

Methods

Study Area and Evaluation of Prey Base

I conducted my research on Newnan's Lake, Alachua County, Florida, during April-September 1985 and 1986. Newnan's Lake, located 15 km east of Gainesville, Florida, is a 2400 ha hyper-eutrophic lake (Shannon and Brezonik 1972) rimmed with baldcypress (Taxodium distichum) and mixed hardwoods. Most of Newnan's Lake is open water, although from May to October much of the lake periphery is covered by coontail (Ceratophyllum spp.) and spatterdock (Nuphar luteum) vegetation.

I used electrofishing to estimate the fish resource base available to ospreys (see review by Reynolds 1983). This technique uses an electrical charge to stun fish for capture and subsequent measurement or determination of desired parameters, and is considered an effective method by which fish abundances can be estimated.

I ran six 15-min electrofishing transects on two consecutive days each month to estimate fish availability. The relative abundance of each fish species was estimated from the capture data, while an index of absolute abundance was calculated from the number of fish captured per 15-min transect. Fish parameters collected included fish species, weight (g), and total length (cm).

Fledgling Foraging Behavior

To aid in identification of young, I climbed suitable nest trees and marked young ospreys with unique color band combinations prior to fledging. I observed fledgling foraging behavior from a boat anchored

offshore at locations that facilitated simultaneous observations on several birds. Individual fledglings were chosen at random and 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 due to difficulties associated with maintaining observation of the same individual, and because it increased the number of independent samples. Instances where either individual or prey type and size class could not be determined were excluded from analysis.

I collected data on osprey foraging behavior during a 10-day period before and one after the 2-day interval during which fish were sampled. Data on prey species and size captured were summarized by individual. To allow comparisons among individuals, I standardized individual foraging data to days since fledging and placed results in 30, 60, 90, 120, and 150-day categories. Each 30-day category was centered around an electrofishing sample. I assumed that variation in fish availability was negligible between the daily sampling periods, and that the number of prey consumed was small relative to the number available.

Identification of prey species captured was relatively straightforward owing to distinctive fish silhouettes and the anterior-posterior manner in which osprey carry fish. I placed prey captured into one of three 10 cm size classes (10-20, 20-30, 30-40) based on relative length of the fish to the bird (see Poole 1982). Size classes of 10 cm represent the best level of resolution I felt capable of identifying.

Analysis

I used log-linear analysis (Agresti 1984) to develop statistical models best describing use of the available fish resource base by ospreys. Log-linear analysis is a procedure similar to analysis-of-variance for use on multidimensional categorical data (e.g., prey size class, age class) (Bishop et al. 1975, Feinberg 1980). Typically, the simplest model that fits the data is considered the most parsimonious. When several models of increasing complexity fit the data, I used conditional tests (Agresti 1984:57-58) to determine the best fit model.

Model cells representing prey captured by each individual osprey were weighted by the relative abundance of each fish species and size class prior to 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, respectively, should not have identical (i.e., 0.5) expected capture probabilities. Instead, capture data needs to be standardized to the relative probability of encounter of each fish species (here, 0.1 and 0.9, respectively).

Standardized lambda estimates were calculated for each cell in the model. Basically, lambda estimates represent 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. Lambda estimates have an asymptotic standard normal distribution and can be compared to normal z -scores for significance testing. Here, I considered significant positive lambda estimates to indicate

"preference" for a particular fish resource type. Non-significant 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).

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

Results

Prey Base

Fish data were collapsed into three categories representing bass (largemouth bass, Micropterus salmoides; striped bass Morone saxtilis), sunfish (warmouth, Lepomis gulosus; bluegill, L. macrochirus; redear sunfish, L. microlophus), and shad (gizzard shad, Dorosoma cepedianum; threadfin shad, D. petenense). Additional fish species, such as the bottom-dwelling brown bullhead (Ictalurus nebulosus) and Florida gar (Lepisosteus platostomus) also were captured during electrofishing bouts, but were excluded from analysis. These species represent prey functionally unavailable for ospreys, and I felt their inclusion in the analysis would bias results by inflating preference measures of other prey.

Prey species were categorized for several reasons. First, fish species placed together are behaviorally and ecologically similar. For instance, all three sunfish interbreed (Breder and Rosen 1966:439-440,

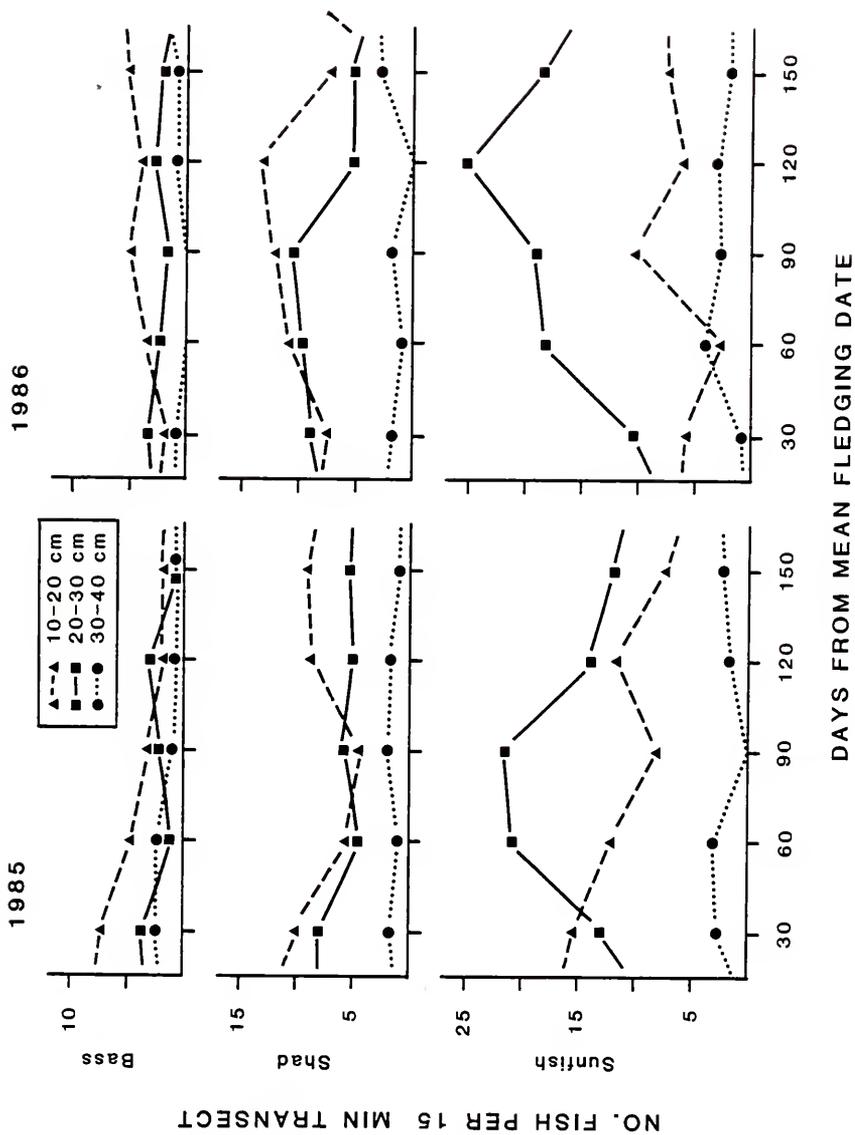
Childers 1967), as do both species of shad (Minckley and Krumholz 1960). Second, foraging habits of the categorized species are similar (references in Breder and Rosen 1966, Carlander 1969, 1977). Last, body forms of grouped fish species are similar, and it is unlikely that ospreys are capable of distinguishing minute differences (e.g., presence of red dot on lateral surface of redear sunfish) between species in the absence of gross behavioral differences. Thus, categories represent groupings based primarily on prey ecology, not taxonomic considerations.

Prey relative abundances varied throughout both years (Fig. 3-1). Sunfish were the predominant species in both seasons, comprising 48-65% and 39-56% of the available prey in 1985 and 1986, respectively. The most common size class was 20-30 cm. Sunfish 30-40 cm in length were relatively uncommon. Shad had the second highest relative abundances in both years. Shad in the 10-20 cm size class increased throughout the post-fledging period, while 20-30 cm sized shad tended to decrease in relative abundance. This most likely reflects the movement of young age class fish from shallow edge waters into the lake at large. Bass were the least common species and exhibited little yearly variation. In general, patterns of change in relative abundance for all three prey categories were similar for both years.

Absolute abundance of fish, measured by the number of fish captured per 15-min electrofishing transect, exhibited patterns of change slightly different from those of change in relative abundance (Fig. 3-2). Bass, for instance, exhibited a gradual decrease in absolute abundance but remained fairly constant in relative abundance in 1985. Most differences between change in absolute and relative abundance

Figure 3-1. Mean relative abundance per 15-min sample transect ($n = 12$) of each prey type and size class during post-fledging periods in 1985 and 1986.

Figure 3-2. Mean number of each prey type and size class captured per 15-min sample transect (n = 12) in 1985 and 1986.



occurred in sunfish in 1985. In May, the relative abundance of sunfish 20-30 cm in length was roughly twice that of the 10-20 cm size class. Absolute abundance, in contrast, was fairly equal, with the 10-20 cm size class only slightly more abundant. Furthermore, during the period May-July when relative abundance of the 10-20 cm size class was constant, absolute abundance steadily decreased. Thus, fledgling ospreys were confronted by an environment whose potential prey resource varied simultaneously in both relative and absolute abundance.

Yearly differences in absolute abundance were more pronounced. With the exception of shad in the 10-20 cm size class, all prey and size class combinations tended to decrease in 1985 and increase in 1986.

Fledgling Foraging Patterns

A total of 11 young in 1985 and 19 young in 1986 were color banded. These birds represented 43% and 37%, respectively, of the yearly reproductive output of the population on Newnan's Lake (Edwards, unpublished data). Due to mortality factors and small sample sizes for some fledglings, data for only 8 young in 1985 and 14 young in 1986 were analyzed (Table 3-1).

Hereafter, short-hand notation will be used to describe the relationship among the factors, where P represents the prey species groups, S the prey size class, T days from the mean fledging date, and B the individual bird. For example, the term PB states that prey choice is associated with individual birds (i.e., the factors are not independent of one another).

Table 3-1. Summary of capture data for 1985 and 1986. Capture data for each time period, fish species and size class cell are collapsed across individuals.

Size Class (cm):	Bass			Shad			Sunfish			Totals
	10-20	20-30	30-40	10-20	20-30	30-40	10-20	20-30	30-40	
1985 (8 birds)										
Time (days)										
30	10	2	0	11	4	0	35	34	0	96
60	15	14	1	18	19	3	35	50	0	155
90	22	17	1	12	15	2	12	34	0	115
120	16	15	0	20	14	1	21	17	0	104
150	16	14	2	25	21	1	18	22	1	120
Totals	79	62	4	86	73	7	121	157	1	590
1986 (14 birds)										
Time (days)										
30	9	11	0	35	31	0	18	42	0	146
60	17	12	0	59	44	0	18	79	0	229
90	17	7	0	47	41	1	31	67	0	211
120	14	13	2	56	14	0	29	81	1	210
150	20	7	1	43	33	0	27	73	2	206
Totals	77	50	3	240	163	1	123	342	3	1002

A variety of models adequately describes the ontogeny of foraging in this population of ospreys (Table 3-2). There exists, however, considerable difference in the adequacy of certain models between years. For example, of the 15 statistically sound models, only PST and PST,PB fit the data in both years. Neither model, however, was the best-fit model in either year. Based on conditional tests (see methods), the best-fit model also differed between years. The remaining models were specific for each year.

Model PS,PB,PT. The best-fit model in 1985 was PS,PB,PT. This model states that choice of prey by fledglings was related to prey size class, individual bird, and time. In contrast, an entirely different model best explained foraging in 1986. This model, PB,ST, states that prey choice was related to individual birds, and that choice of size class was related to time.

Use of the available size classes by fledglings in 1985 was non-random, with young essentially ignoring fish 30-40 cm in length ($\lambda = -1.014$, $SE = 0.101$, $P < 0.001$). Use of the remaining two size classes was at a rate greater than that expected at random (10-20 cm, $\lambda = 0.517$, $SE = 0.064$, $P < 0.001$; 20-30 cm, $\lambda = 0.497$, $SE = 0.066$, $P < 0.001$). In contrast, all three prey groups were captured at random.

Examination of the PS interaction term reveals that difference in use of size class was associated with sunfish (Table 3-3). Young tended to use sunfish 20-30 cm in length at rates greater than expected at random and ignored the larger-sized sunfish. The remaining prey groups and size classes did not differ from random. Young apparently used

Table 3-2. Summary of models fitting foraging patterns of recently fledged ospreys in 1985 and 1986. Missing values indicate a particular model did not adequately fit the data for that year. Conditional tests were used to determine the best-fit model for each year. Best-fit models for 1985 and 1986 were PS,PB,PT and PB,ST, respectively. See text for explanation of model terms.

Model	Description	1985		1986	
		G ²	df	G ²	df
ST	choice of size class related to time.	-	-	348	522
ST,P	choice of size class related to time; varies over prey.	-	-	334	520
PB	bird.	-	-	305	495
PB,PS	bird; size class.	245	271	-	-
PB,S	bird; varies over size class.	-	-	298	493
PB,ST	bird; choice of size class related to time.	-	-	267	481
PS,PT	size class; time.	223	280	-	-
PS,BT	size class; choice by bird related to time.	234	257	-	-
PS,PB,PT	size class; bird; time.	169	259	-	-
PS,PT,BT	size class; time; choice by bird related to time.	177	249	-	-
PS,PB,PT,BT	size class; bird; time; choice by bird related to time.	136	235	-	-
PST	both size class and time.	183	259	290	495
PST,PB	both size class and time; bird.	129	238	233	456
PST,BT	both size class and time; choice by bird related to time.	137	228	-	-
PST,PB,BT	both size class and time; bird; choice by bird related to time.	97	214	-	-

Table 3-3. Lambda estimates and SE's for the best-fit model PS,PB,PT in 1985. Standardized lambda estimates can be obtained by dividing each lambda estimate by its SE. Positive and negative signs show direction of preference; significant estimates signify use at a rate greater or less than that expected at random. Superscripted birds with the same number indicate siblings.

Prey-Size Interaction Term (<u>PS</u>)						
Size	Bass		Shad		Sunfish	
	lambda	SE	lambda	SE	lambda	SE
10-20 cm	0.007	0.096	-0.037	0.088	0.030*	0.092
20-30 cm	0.111	0.140	0.195	0.131	-0.306**	0.154
30-40 cm	-0.118	0.096	-0.158	0.088	0.276**	0.093

Prey-Bird Interaction Term (<u>PB</u>)						
Bird	Bass		Shad		Sunfish	
	lambda	SE	lambda	SE	lambda	SE
J01-85 ₁	-0.191	0.173	0.322*	0.148	-0.131***	0.147
J02-85 ₁	-0.264	0.161	-0.242	0.152	0.506**	0.125
J03-85 ₂	-0.219	0.161	-0.155	0.151	0.374**	0.128
J04-85 ₂	0.220	0.130	0.017	0.121	-0.237	0.126
J05-85 ₂	0.251	0.141	0.012*	0.146	-0.263	0.138
J06-85	-0.255**	0.188	-0.320*	0.162	-0.065	0.153
J07-85	0.389	0.130	-0.164	0.138	-0.225	0.130
J08-85	0.069	0.175	-0.110	0.168	0.041	0.152

Prey-Time Interaction Term (<u>PT</u>)						
Time	Bass		Shad		Sunfish	
	lambda	SE	lambda	SE	lambda	SE
30	-0.287*	0.143	-0.209	0.132	0.497***	0.109
60	-0.125*	0.111	-0.072	0.106	0.197*	0.093
90	0.260*	0.111	-0.151	0.115	-0.109*	0.106
120	0.111	0.120	0.171*	0.117	-0.283**	0.112
150	0.041	0.116	0.261*	0.107	-0.301	0.105

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

these prey and size class combinations in relation to their availability.

The presence of a PB interaction term suggests that considerable variation exists among individual birds and their use of the available prey resources. Four of the eight banded young in 1985 captured fish in relation to their availability, while two concentrated on sunfish. The remaining two birds concentrated on shad and bass, respectively. An unexpected pattern was the lack of difference in preference between siblings, even though there existed differences in how the sib-groups used prey. Siblings J02-85 and J03-85 did not differ statistically in their use of bass ($\underline{z} = -0.72$, $\underline{p} > 0.05$), shad ($\underline{z} = -1.69$, $\underline{p} > 0.05$) or sunfish ($\underline{z} = -1.80$, $\underline{p} > 0.05$), although both young exhibited preference for sunfish (Table 3-3). Similarly, siblings J04-85 and J05-85 had identical preference patterns (bass, $\underline{z} = 0.28$; shad, $\underline{z} = 0.49$; sunfish, $\underline{z} = 1.03$; $\underline{p} > 0.05$ for all three prey types). They did not, however, exhibit preference for any prey type and instead used prey in relation to their abundance.

The relationship between prey and time since fledging (PT) shows a strong pattern of change, with young initially ignoring bass and concentrating on sunfish. By 150 days into the post-fledging period, however, young had changed emphasis and were exhibiting preference towards shad.

Model PB,ST. Although a different model, PB,ST, met the best-fit criteria for 1986, there exist some similarities in model terms between years. Young in 1986 also ignored fish 30-40 cm in length ($\lambda = -1.185$, $SE = 0.077$, $\underline{p} < 0.001$) and exhibited strong preference

for both the 10-20 cm ($\lambda = 0.509$, $SE = 0.05$, $P < 0.001$) and 20-30 cm size classes ($\lambda = 0.676$, $SE = 0.048$, $P < 0.001$).

The presence of a PB interaction suggests, as in 1985, that there existed considerable variation in preference among young (Table 3-4). Ten of 14 young used the available prey at random, although examination of lambda estimate signs indicates considerable variability among young in the direction of preference. Three birds, J06-86, J09-86, and J13-86, showed strong preference for shad, taking this prey at a rate greater than expected at random. Only J04-86 exhibited preference for bass. In contrast to 1985, where preference for prey was divided roughly among young, the majority of young in 1986 used available prey in relation to their availability.

Siblings again exhibited similar preference patterns. Young J04-86 and J05-86 did not differ in their use of bass ($z = -1.28$, $P > 0.05$), shad ($z = -1.10$, $P > 0.05$), and sunfish ($z = 0.22$, $P > 0.05$). Siblings from one nest, however, did differ slightly. Fledgling J04-86 exhibited strong preference for bass while its sibling, J05-86, did not. Comparison of the lambda estimates, however, revealed that the difference in use of bass between the two siblings was not significant ($z = 0.88$, $P > 0.05$). Preference for shad ($z = -0.94$, $P > 0.05$) and sunfish ($z = 0.36$, $P > 0.05$) also did not differ.

Unlike the best-fit model for 1985, there was no PI interaction term in 1986. Instead, preference for particular prey types remained constant throughout the entire post-fledging period. Both shad ($\lambda = 0.188$, $SE = 0.044$, $P < 0.001$) and sunfish ($\lambda = 0.4$,

Table 3-4. Lambda estimates and SE's for the best-fit model PB,ST in 1986. Standardized lambda estimates can be obtained by dividing each lambda estimate by its SE. Positive and negative signs show direction of preference; significant values signify use at a rate greater or less than that expected at random. Superscripted birds with the same number are siblings.

Prey-Bird Interaction Term (<u>PB</u>)						
Bird	Bass		Shad		Sunfish	
	lambda	SE	lambda	SE	lambda	SE
J01-86	-0.033	0.166	-0.028	0.131	0.061	0.126
J02-86	0.003	0.150	-0.119	0.138	0.116	0.128
J03-86	-0.082*	0.236	-0.022	0.183	0.104	0.176
J04-86 ¹	0.348	0.167	-0.269	0.156	-0.079	0.143
J05-86 ¹	0.288	0.155	-0.188*	0.140	-0.100	0.131
J06-86 ²	-0.076	0.179	0.300*	0.134	-0.224	0.142
J07-86 ²	0.072	0.181	-0.282*	0.141	0.211	0.138
J08-86 ²	0.164	0.204	-0.373*	0.188	0.209	0.160
J09-86	-0.250	0.194	0.280	0.140	-0.030	0.140
J10-86	0.270	0.165	-0.165	0.147	-0.105	0.140
J11-86	-0.066	0.175	0.166	0.134	-0.100	0.134
J12-86	-0.151*	0.188	0.259***	0.140	-0.108	0.144
J13-86	-0.469*	0.229	0.601***	0.151	-0.132	0.162
J14-86	-0.018	0.254	-0.160	0.207	0.178	0.190

Size-Time Interaction (<u>ST</u>)						
Time	Size					
	10-20 cm		20-30 cm		30-40 cm	
	lambda	SE	lambda	SE	lambda	SE
30	-0.197*	0.100	-0.164	0.095	0.361*	0.146
60	0.162	0.102	0.105	0.099	-0.267	0.166
90	0.060	0.099	0.061	0.096	-0.121	0.158
120	0.011	0.100	-0.045	0.098	0.034	0.159
150	-0.036	0.093	0.043	0.090	-0.007	0.135

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

SE = 0.044, $P < 0.001$) were preferred prey types, while bass were ignored ($\lambda = -0.588$, SE = 0.054, $P < 0.001$).

Patterns derived from the ST interaction are less clear. Difference in use of the available prey size classes appears restricted to the first 30 days of post-fledging, when young exhibited strong preference for the smallest size class. Fish in the 30-40 cm size class were ignored.

Fledgling Versus Adult Foraging Patterns

Comparison of use of available prey by young with adults revealed differences in learning curves between years, even though young of both years eventually exhibited patterns of prey preference similar to that of adults. Implicit in these results is the assumption that adults represent some baseline of proficiency that is better than that exhibited by naive fledglings.

Examination of change in preference of young in 1985 revealed a gradual shift in choice, until by 150 days young were foraging in a manner similar to adults (Fig. 3-3). There exist, however, differences in the length of time required to reach the level of preference exhibited by adults for each prey class. Young fell within confidence limits of adult preference for bass by 90 days, while it took 150 days to attain preference levels exhibited for shad and sunfish. Use of prey size classes also differed between adults and fledglings in 1985 (Table 3-5). In general, young captured smaller size class prey than did adults.

Figure 3-3. Change in preference of available prey types by fledglings (solid squares) in 1985 in relation to time. Rectangles represent 95% confidence intervals about the lambda estimates of adult data fitted to the model $PS_{PB,PI}$. Asterisks represent significant difference in preference patterns between young and adults.

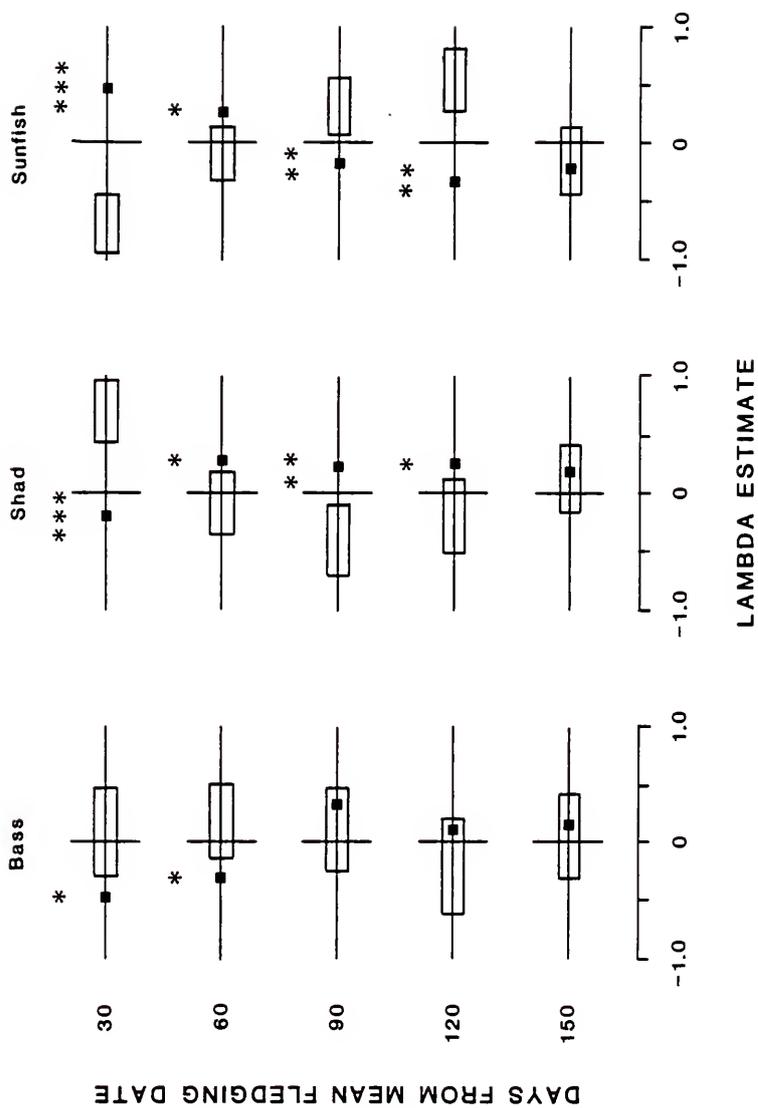


Table 3-5. Lambda estimates and SE's for adult data fitted to the best-fit model PS,PB,PT in 1985. Positive and negative signs within parentheses indicate significant difference in use of particular prey and size class combinations between young and adults. Signs also indicate direction of preference.

Adult Prey-Size Interaction Term (<u>PS</u>)						
Size	Bass		Shad		Sunfish	
	lambda	SE	lambda	SE	lambda	SE
10-20 cm	0.207	0.145	-0.260 (+)	0.108	0.054	0.134
20-30 cm	0.583 (-)	0.233	0.129	0.181	-0.713	0.241
30-40 cm	-0.790 (+)	0.181	0.131 (-)	0.121	0.659 (-)	0.144

The lack of a PT interaction in the best-fit model for 1986 implies that no relationship existed between time since fledging and prey choice in young. Young exhibited the same pattern of prey preference from fledging until they dispersed from the area, and did not differ from adults in use of prey (bass, $\underline{z} = -1.44$, $\underline{P} > 0.0$; shad, $\underline{z} = 1.88$, $\underline{P} > 0.05$; shad, $\underline{z} = 1.453$, $\underline{P} > 0.05$) at any time during the post-fledging period. In contrast to 1985, prey preference patterns of young in 1986 did not differ from that exhibited by adults during the same time period.

Discussion

The lack of similarity in best-fit models between years suggests that no one pattern best describes the ontogeny of foraging in this population of ospreys. This difference may be due to between year differences in prey absolute and relative abundance.

Young in 1985 exhibited a strong temporal shift in preference, changing from preference for sunfish soon after fledging to shad by the end of the post-fledging period. Initially, sunfish were the most abundant prey type. By 150 days, however, the absolute abundance of sunfish had decreased, and young were concentrating on shad. The switch to shad parallels an increase in their absolute abundance. Choice by young ospreys reflects these changes in absolute abundance, suggesting that young may be more sensitive to absolute than to relative abundance of prey.

Sensitivity to change in prey absolute abundance is a factor common to foraging models concerned with energy optimization (MacArthur and Pianka 1966, Schoener 1971, Pulliam 1974, Werner and Hall 1974, Charnov 1976a). These models predict that an increase in absolute abundance of preferred prey results in an increased representation of those prey types in the diet. While it is tempting to conclude that young ospreys foraged in a manner consistent with energy-optimizing models, several factors make such a conclusion tenuous at best.

A major complication is that my results also provide general support for prey switching models. These models (Murdoch 1969, 1973, Murdoch and Oaten 1975) predict a shift in preference as relative abundance changes, with predators concentrating on the most abundant prey type. Because shifts in relative abundance in 1985 roughly parallel shifts in absolute abundance (Figs. 2-1 and 2-2), it is difficult to ascertain whether young are responding to change in absolute (energy-optimizing) or relative (nutrient-optimizing) abundance.

Second, it frequently is difficult to determine the preferred or "higher-ranked" prey from an energetic sense. Here, for instance, I was unable to determine if costs (e.g., handling) and benefits differed among the available prey types. While it is easy to define preference based on observations of choice by young ospreys, it is difficult to determine a priori whether sunfish represent "higher-ranked" prey. Last, it is unlikely that naive young know what constitutes "higher-ranked" prey when they fledge. Such knowledge requires a fairly rigid genetic basis that is not likely in a species confronting a

variable environment (Glasser 1982, 1984; Glasser and Price 1982). It is more likely that young ospreys are simply exhibiting preference for the most common prey type, initially selecting for sunfish due to their high absolute and relative abundance. Similarly, the shift in preference to shad was associated with a concurrent increase in its absolute and relative abundance. Both shifts in preference indicate a high degree of flexibility in preference patterns of young ospreys.

Evidence for flexibility in foraging within this population of ospreys is strengthened by results from 1986. The lack of a PT interaction in this year implies choice of prey by young was constant over the course of post-fledging. Thus, although absolute and relative abundance of prey types and size classes varied over the post-fledging period, choice by young remained constant. Constant preference for prey types irrespective of variation in prey abundance is an explicit prediction of foraging models based on nutrient constraints (Marten 1973, Pulliam 1975, Westoby 1978). That results from different years tend to support different groups of foraging models is not surprising, and lends credence to the concept that prey choice should vary with fluctuations in the prey resource base. Predators, and in particular young in the process of developing foraging skills, should not be expected to operate within the constraints of particular foraging models. Young birds, for instance, require a certain degree of flexibility so they can react to whatever environmental conditions they initially face. Such flexibility, particularly as it relates to the ability to respond to new or highly variable environments, is clearly

advantageous to a species whose young must soon migrate from the natal area.

A common factor to the best-fit models of both years was the PB interaction term. This term suggests individuals differed in use of the available prey types (see also Murdoch and Oaten 1975, Chesson 1984). The presence of a PI interaction term in 1985 also suggests this individual variation in preference was related to time. The lack of a PI interaction in 1986, however, suggests that individual young did not change preference over time. Instead, differences among young were constant over time. Whether these differences among young, with some individuals foraging at random and others exhibiting strong preference for one or more prey types, affect subsequent survivorship is not known. Clearly, flexibility in foraging exists both at a population level between years, and among young within each year.

Learning curves of young also differed between years. Young in 1985 did not attain preference patterns of adults until at least 120 days into the post-fledging period. Learning curves in this year showed shifts in preference over time. In contrast, young in 1986 almost immediately "locked into" the foraging patterns of adults, and did not vary preference patterns throughout post-fledging. A contributing factor to this difference in learning curves may be between year differences in prey abundance.

Prey abundance in 1986 was increasing when young fledged. An increase in the number of available prey during the period young are developing foraging skills may increase encounter rates, thereby allowing for finer discrimination among prey types. The ability to

discriminate may develop if young are able to retain whatever cues led to a successful foraging bout. Retention of successful cues may represent a variation of the "win-stay, lose-shift" response strategy common in the learning set literature (e.g., Levine 1959). Although its ecological application has been primarily to predator patch choice (e.g., Cole et al. 1982, Wunderle and O'Brien 1985), the principle of repeating when successful or avoiding when unsuccessful is applicable to the development of preference for prey in naive young. A constant or increasing prey resource provides young with the opportunity to rapidly develop discrimination for prey types, even if foraging skills, as measured by indices such as capture success, are low.

In contrast to 1986, decreasing prey abundance in 1985 may have forced young ospreys to abandon regularly whatever cues developed from a "win-stay, lose-shift" strategy. Rewards were not sufficiently consistent to warrant cue retention. Even if successful cues were retained, lower encounter rates may have made it difficult for young to exhibit constant preference for particular prey types. Lower encounter rates coupled with lower success rates may have forced young to begin sampling again instead of waiting for cues associated with "win-stay." Subsequent successful capture of a different prey type would lead to the retention of an entirely new set of cues. Thus, change in preference over time may represent shifts in learning sets as young are constantly forced to acquire new cues.

CHAPTER IV

SIBLING ENHANCED FORAGING IN OSPREYS

Introduction

Differences in the foraging ability of adult and young birds have been documented for a variety of avian species (references in Brandt 1984). One explanation may be that the coordination and motor skills of young are not fully developed. Consequently, young may be less effective than adults in the mechanics of prey capture (e.g., Ingolfsson and Estrella 1978, Brandt 1984). Alternatively, young may be as proficient as adults in the mechanics of foraging, but lack knowledge of available resources (e.g., Davies and Green 1976). Young simply have not had sufficient opportunity to encounter prey items and assimilate cues leading to successful foraging behaviors.

Here, I examine the role of social relationships in shaping the development of foraging skills in fledgling ospreys (Pandion haliaetus). An important component of this process may be potential benefits derived from interactions with other young and adult ospreys. One benefit of sociality may be an increased rate of learning due to the more frequent exposure to successful foraging cues. In contrast, young learning to forage without the opportunity to interact with conspecifics may develop foraging skills at a slower rate.

I also examine the nature of interactions among young and between adult and young ospreys during the post-fledging period. One factor thought to influence foraging performance is competition (MacArthur 1972, Werner 1976), and young ospreys might be expected to exhibit considerable aggression towards other young or adults if resource availability is low or if they initially have a difficult time capturing prey. If, however, there exist benefits related to observational learning, then the frequency of aggressive interactions between young might be lower.

Study Area and Methods

My research was conducted on Newnan' Lake, Alachua County, Florida, during April-September 1985 and 1986. Newnan's Lake, located 15 km east of Gainesville, Florida, is a 2400 ha hyper-eutrophic lake (Shannon and Brezonik 1972) rimmed with baldcypress (Taxodium distichum) and mixed hardwoods. Most of Newnan's Lake is open water, although from May to October much of the lake periphery is covered by coontail (Ceratophyllum spp.) and spatterdock (Nuphar luteum) vegetation.

To identify young, I climbed suitable nest trees and marked nestling ospreys with unique color band combinations prior to fledging. I collected data on fledgling ospreys from a boat anchored offshore at locations that facilitated simultaneous observations on several birds. Individual fledglings were chosen at random and watched until the completion of a 15-min period or until a successful capture was made. I preferred this approach over continuous observations due to difficulties

associated with maintaining observation of the same individual, and because it increased the number of independent samples. Instances where I was unable to identify individuals could were excluded from analysis.

Observations were collected during two 10-day periods each month. Behavioral observations were standardized to days since fledging for each bird and placed in 30, 60, 90, 120, and 150-day categories. I considered young to have fledged once they left the nest tree.

Hereafter, "related" refers to two young from the same nest and "sibling-group" to related birds engaged in social or hunting activities together. "Unrelated" birds were those from single chick nests. "Solo" refers to a hunting flight by a single bird; "tandem-hunt" to hunts where more than one bird participated in a hunting flight. Both related and unrelated birds participated in solo and tandem-hunt flights. Criteria defining participation included close (<10 m) proximity, similar flight direction and foraging height, and capture attempts by all birds directed towards the same prey item. Observation of a tandem-hunt was terminated if one of the birds broke off hunting and left the area.

A capture attempt included any stooping effort that brought the bird within 3 m of the water surface. I defined successful capture as the capture and retention of a prey item for at least 15 s or until the bird landed in a tree to begin feeding. Unsuccessful capture attempts included any attempt at capture that failed to result in retention of a prey item. Loss of prey items within the first 15 s was due primarily to pirating attempts by other birds or the inability of the bird to

grasp and control the fish. I excluded losses of this nature from the calculation of individual capture success rates.

Multiple attempts for the same prey item each constituted one capture attempt. I evaluated capture attempts by sibling-groups in two ways. First, capture success was evaluated for the sibling-group. As before, each attempt by a bird during a tandem-hunt was counted. I also calculated the capture success of each individual involved in a tandem-hunt.

Data were analyzed using weighted G-tests (Sokal and Rohlf 1981). The level of significance for all analyses was 0.05.

Results

A total of 11 young in 1985 and 19 young in 1986 were color banded. Due to mortality factors and small sample sizes for some fledglings, data for only 8 young in 1985 and 14 young in 1986 were analyzed. Fledgling ospreys attempted to capture prey as early as five days after fledging, but the earliest successful capture I observed was 11 days after fledging. All banded birds had made at least one successful capture by 20 days into the post-fledging period.

Capture success for each 30-day category did not differ between years for either related or unrelated young. Consequently, data for both years were combined for analysis. Capture success of ("related") sibling-groups and ("unrelated") lone ospreys was initially similar, but by 60 days from the mean fledging date sibling-groups were more successful at capturing prey than were lone ospreys (Table 4-1).

Table 4-1. Comparison of capture success by related and unrelated fledgling ospreys in relation to days from mean fledging date (DMFD). Data for 1985 and 1986 did not differ for each 30-day category and were combined for analysis. A = Number capture attempts observed; S = Number successful captures.

DMFD	Related			Unrelated			z-score
	A	S	(%)	A	S	(%)	
30	333	73	(21.9)	742	162	(21.8)	0.03
60	388	132	(34.0)	838	234	(27.9)	2.17 [*]
90	181	104	(57.4)	687	283	(41.2)	3.90 ^{***}
120	194	133	(68.6)	351	181	(51.6)	3.84 ^{***}
150	214	143	(66.8)	313	183	(58.5)	1.92

^{*} $\underline{P} < 0.05$; ^{***} $\underline{P} < 0.001$

Differences were greatest at 90 days post-fledging. Capture success of both groups was statistically similar by 150 days, although capture success of lone birds was still lower than that of sibling-groups.

Differences also existed in the time required until capture success of young was similar to that of adults. Capture success by sibling-groups approached that of adults at a faster rate than that exhibited by unrelated birds foraging by themselves (Fig. 4-1).

Capture success also varied with type of hunting (Table 4-2). More than 80% of the capture attempts by related birds occurred during tandem hunts. Birds with siblings seldom hunted by themselves. In contrast, even though unrelated birds occasionally hunted and attempted to capture prey together, more than 90% of capture attempts by lone birds occurred during solo hunts. Unrelated birds seldom remained in close proximity to one another, particularly during hunting flights. Capture success by unrelated birds hunting in tandem was consistently lower than that of unrelated birds hunting singly (Table 4-2), although differences were not significant ($P > 0.05$ for each 30-day category). Capture success by related birds was similar regardless whether they hunted in tandem or singly.

Young tended to remain near and interact with adults during the first 30-60 days post-fledging (Fig. 4-2). As the post-fledging period progressed, young interacted less with adults and more with other young. The number of observed interactions dropped considerably just prior to the time young dispersed from the area.

The nature of interactions between adults and young and between young varied over the post-fledging period. In general, interactions

Figure 4-1. Mean capture success of related and unrelated ospreys compared to 95% confidence intervals about adult capture success during the same time period. Data for 1985 and 1986 are combined.

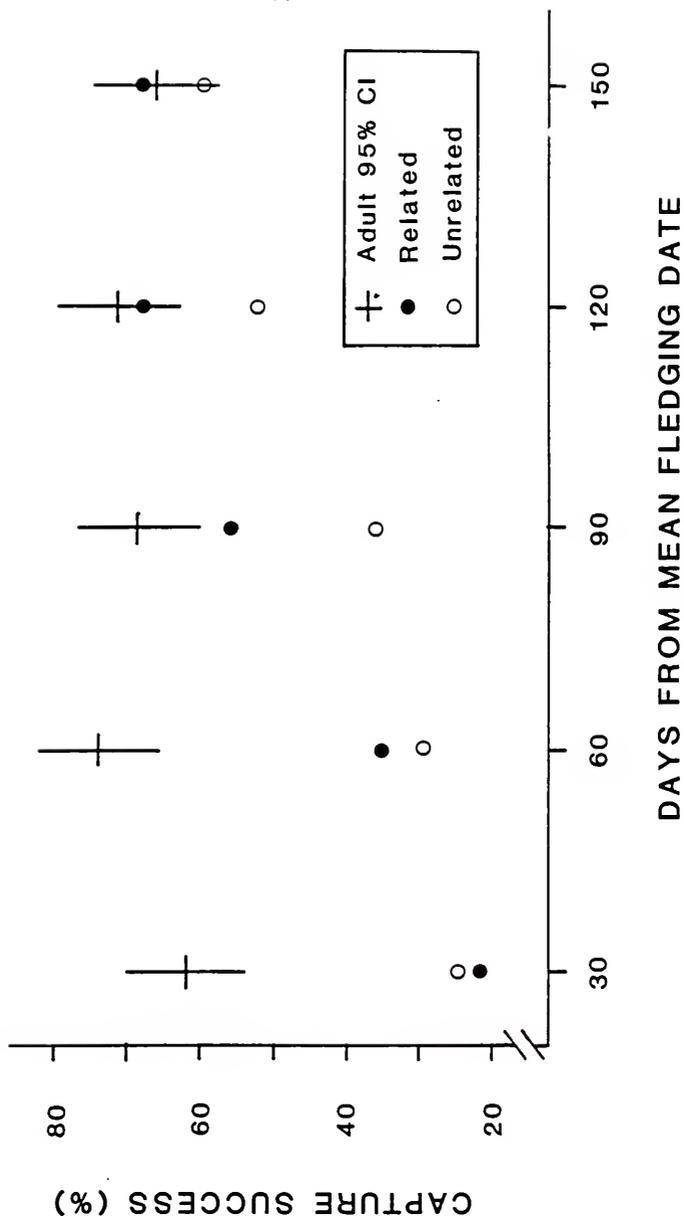
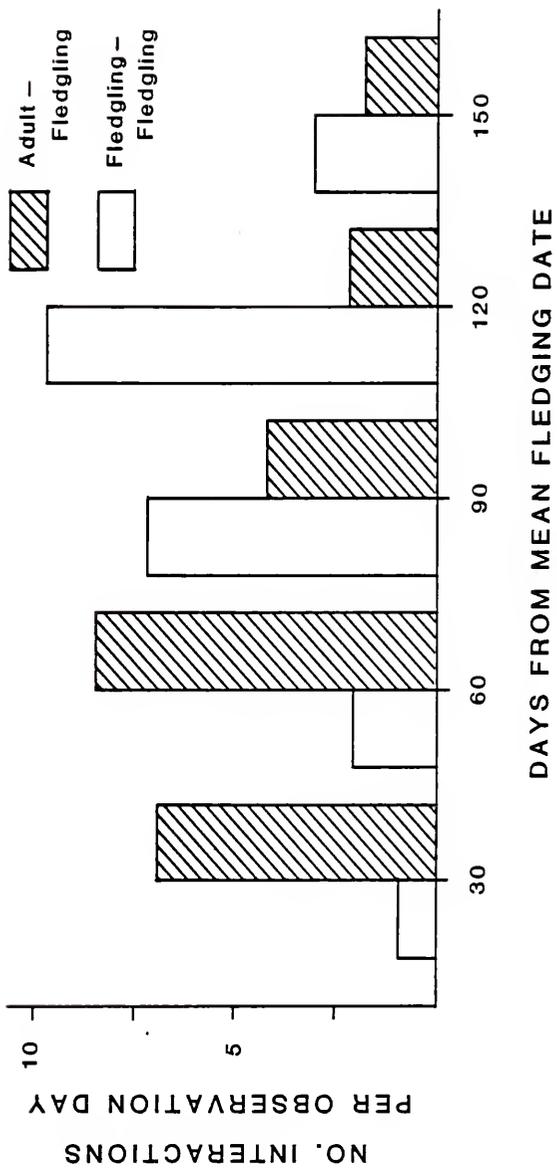


Table 4-2. Comparison of tandem and solo hunt capture success of related and unrelated fledgling ospreys in relation to days from mean fledging date (DMFD). Data for 1985 and 1986 are combined. A = Number capture attempts observed; S = Number successful captures.

DMFD	Tandem Hunts				Solo Hunts				z-score
	Related		Unrelated		Related		Unrelated		
	A	S (%)	A	S (%)	A	S (%)	A	S (%)	
30	297	64 (21.5)	27	4 (14.8)	36	9 (25.0)	715	158 (22.1)	0.39
60	332	114 (34.3)	41	12 (29.3)	56	18 (32.1)	797	222 (27.8)	0.67
90	159	93 (58.4)	58	19 (32.8)	22	11 (50.0)	629	264 (41.9)	0.75
120	155	106 (68.4)	42	19 (45.2)	39	27 (69.2)	309	162 (52.4)	2.12*
150	126	85 (67.5)	37	19 (51.4)	88	58 (65.9)	276	164 (59.4)	1.11

* $\underline{p} < 0.05$; ** $\underline{p} < 0.01$; *** $\underline{p} < 0.001$

Figure 4-2. Number of observed fledgling-fledgling and adult-fledgling interactions in relation to days from mean fledging date. Number of interactions is weighted by sample effort. Data for 1985 and 1986 are combined.



between young were more aggressive than affiliative in nature. Aggressive actions directed towards other young included pirating attempts, perch displacements, and beak and foot stabs. Of interest, however, is the large difference in the proportion of aggressive interactions initiated between related and unrelated young (Table 4-3). Related birds had fewer aggressive interactions with other young than did unrelated birds, even though related birds were in the proximity of one another more often than related birds met. Roughly 90% (50 of 55) of observed aggressive interactions between related young involved fights over a prey item captured by, or in the possession of, one of the young.

In contrast, related and unrelated birds did not differ greatly in the manner in which they interacted with adults (Table 4-3). Interactions with adults were more aggressive than interactions with other fledglings. Unlike fledgling-fledgling interactions, however, aggressive interactions with adults primarily involved attempts to pirate prey. Young rarely attempted to displace adults from perches or initiate other kinds of aggressive interactions.

Discussion

There exist several processes by which naive young incorporate information from initial foraging bouts into a successful foraging strategy. One method is trial and error, often referred to as a "win-stay, lose-shift" response strategy in some learning set literature (Levine 1959, Kamil and Yoerg 1982). Through repeated sampling of their

Table 4-3. Frequency of aggressive interactions between fledglings and between fledgling and adult ospreys in relation to days from mean fledging date (DMFD). Fledglings are categorized as either related or unrelated (see text). Data for 1985 and 1986 are combined. T = Total number of affiliative and aggressive interactions observed; N = Number of aggressive interactions observed.

DMFD	Unrelated			Related			z-score
	T	N	(%)	T	N	(%)	
Fledgling-Fledgling Interactions							
30	13	8	(61.5)	10	3	(30.0)	1.59
60	23	17	(73.9)	15	5	(33.3)	2.66**
90	89	45	(50.6)	55	14	(25.4)	3.19**
120	125	59	(47.2)	67	23	(34.3)	1.76
150	32	14	(43.8)	29	10	(34.5)	0.75
Adult-Fledgling Interactions							
30	91	72	(79.1)	47	34	(72.3)	0.87
60	96	78	(81.2)	69	61	(88.4)	-1.29
90	53	33	(62.3)	34	28	(82.3)	-2.14*
120	25	13	(52.0)	17	7	(41.2)	0.69
150	26	7	(26.9)	11	4	(36.4)	-0.56

* $\underline{P} < 0.05$; ** $\underline{P} < 0.01$

environment, young eventually learn to recognize and retain cues associated with successful foraging bouts. Cues associated with unsuccessful foraging bouts are not retained. Another method increasing foraging ability is observational learning (Turner 1964), whereby naive birds use conspecifics as role models. Here, birds not only learn through individual trial and error, but also by simultaneously observing and retaining those cues leading to successful foraging bouts by other birds. Observational learning, when possible, is considered a more efficient method than trial and error for developing the skills necessary to exploit novel resources (Galef 1976).

The importance of observational learning in the development of foraging behavior in fledgling ospreys can only be inferred from the data presented here. That it plays some role, however, is supported by several lines of evidence. First, even though considerable variation in how fledglings used available resources existed, siblings, who tended to remain together throughout the post-fledging period, had similar patterns of prey preference (Chapter III). In addition, related birds hunting together not only had greater success at capturing prey, but their success rate also approached that of adults at a faster rate than that exhibited by unrelated birds. The more rapid development of foraging skills in naive young having opportunity for observational learning has been documented for a variety of bird (Turner 1964, Dawson and Foss 1965, Alcock 1969) and mammal species (references in Weigl and Hanson 1980). In general, role models in these studies were experienced animals presumably foraging at some optimal level. Naive animals apparently learned appropriate foraging techniques through observation.

In contrast, it appears that naive ospreys are capable of learning appropriate foraging behaviors from other inexperienced birds as well as from experienced birds. The rapid increase in capture success by related birds foraging together suggests that exposure to mistakes may be as beneficial as exposure to successful capture attempts, even when the individual bird is not directly involved in the capture attempt.

Rapid development of foraging behaviors by young ospreys may be important for several reasons. Although the majority of adults at Newnan's Lake are year-around residents, young of each year disperse from the area by roughly 150 days post-fledging and presumably migrate to Central America. Birds having properly developed foraging skills may have increased survivorship during migration relative to those that do not, particularly since migrating birds continuously face new and different foraging environments.

Different foraging environments also require rapid recognition of potential prey items. Davies and Green (1976) showed that for the Reed Warbler (Acrocephalus scirpaceus) the main factor limiting foraging performance was not mechanics, but rather recognition that flies constituted food items. Migrating ospreys undoubtedly face similar prey recognition problems, and may require a period of adjustment when they encounter a new foraging environment. Observations that related young learn to recognize profitable prey sooner than unrelated young (Chapter III) suggest that observational learning not only aids development of foraging mechanics, but also prey identification. The rapidity with which migrating birds learn to recognize profitable prey items could, as before, affect survivorship, particularly when temporal constraints on

the migration period exist. Whether related young ospreys remain together through all or any part of migration, however, is not known.

The decreased frequency of aggressive interactions between related young also suggests there exists some level of cooperation between related birds. The level of aggressive interactions between related young remained fairly low and constant throughout post-fledging. Aggressive interactions between unrelated young were high initially, but decreased to a level similar for related young by 150 days post-fledging. Decreased aggression between related young may be necessary to realize benefits associated with social foraging (e.g., Pulliam 1973, Bertram 1978). Although predatory birds such as ospreys rarely "flock" together, social foraging or "conspecific cueing" (Kiestler and Sklatkin 1974) by related birds may increase levels of prey detection. Benefits related to predator avoidance are not applicable to ospreys. Similar levels of aggression between related and unrelated young once a prey item is captured, however, suggest that any cooperation between related birds is transitory.

CHAPTER V

CONCLUSION AND SYNTHESIS

While the concept of a facultative foraging strategy generally describes the foraging behavior of this population of ospreys, my observations do not entirely corroborate the concept as outlined by Glasser (1982, 1984). They do, however, suggest it provides a more general framework in which foraging behaviors can be evaluated. Unfortunately, increased generality decreases the utility of the concept as a rigorous approach to understanding foraging behaviors, a not uncommon criticism of many foraging models. Moreover, the predictions Glasser (1982, 1984) generates are not mutually exclusive from other model predictions (e.g., Schoener 1971, Pulliam 1974).

My findings that ospreys change prey preference throughout the year are not new. These observations, however, are enhanced by my extensive documentation of the dynamics of the fish resource base. The strong association between changes in the fish resource base and shifts in prey preference suggests that adult ospreys at least are capable of modifying foraging behavior in response to changing resource conditions. Whether these seasonal shifts from a generalist strategy in pelagic habitat to a specialist strategy in littoral habitat

constitute an "optimal" foraging strategy that maximizes fitness is debatable.

Problems abound in current optimal foraging literature, ranging from serious criticism that it is tautological (Ollason 1980) to questions whether an optimal framework is even necessary to understand foraging behavior (Heinrich 1983). That my results adequately fit a variety of proposed models provides additional evidence that many foraging models are too narrowly defined. To attempt to force my results into a particular model adds little understanding to foraging behavior, except to generate yet another set of ad hoc explanations for deviations from model predictions. The ecology of osprey foraging behavior may be understood best by using the heuristic value of optimal foraging theory as a framework for interpretation of results.

In particular, my interpretation of the shift from one foraging strategy to another was confounded by the presence of time lags. These temporal lags in change of preference are not unlikely in predators foraging in variable environments, and may be due to delay in the 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. Consequently, predators may continue to capture less profitable prey types until a new search image is formed. Similarly, the time required to develop a new search image could explain why ospreys here did not immediately respond to increases in the abundance of sunfish. Instead, change in preference was gradual. Thus, rather than the abrupt shift in preference predicted by

some foraging models (e.g., Krebs et al. 1978), change in preference could occur gradually. Lag in preference could simply represent time required to develop a new search images appropriate for a different resource base.

Habitat switches exhibited by my study population suggest an opportunistic response by ospreys to increases in prey abundance. Ospreys switched from foraging in pelagic to littoral habitat when prey abundances in the littoral habitat increased and exceeded those in pelagic habitat. The regularity associated with this pattern suggests some form of frequency-dependent diet (Fullick and Greenwood 1979, Horsley et al. 1979) best may describe osprey foraging. That temporal lags do not disappear between years suggests that some form of memory decay regarding preference occurs between years. Apparently, constant reinforcement of a specific search image is necessary to maintain adequate levels of prey detection (Pietrewicz and Kamil 1979, McNair 1981).

Temporal variation in the prey resource base also played an important role in the ontogeny of foraging in this population of ospreys. Differences in developmental patterns were strongly associated with between-year differences in the prey resource base. Decreasing prey abundance during the post-fledging period in 1985 extended the learning period by making it difficult for young to develop appropriate learning sets. In contrast, increasing prey abundance during 1986 shortened the learning period. Apparently, naive ospreys require constant reinforcement of cues associated with

particular prey types before specific search images for prey can develop.

There appears to be greater flexibility in diet choice than in the mechanics of foraging. For instance, data related to the mechanics of foraging (e.g., capture success) were more constant between years than were estimates of prey preference. Such flexibility in the ontogeny of diet choice is, of course, beneficial to naive predators entering variable environments. In contrast, mechanical aspects of foraging behavior should not be expected to exhibit such variation. Their importance to survival dictates they rapidly be incorporated into a predator's behavioral repertoire.

Social behavior also affected how ospreys developed foraging skills. Faster rates of learning occurred when young had opportunity to interact with other young. Because all young studied here eventually attained foraging skills comparable to adults, benefits associated with faster learning are hard to envision. Such may not be the case for osprey populations farther north, where shorter summers result in shorter post-fledging periods. There, considerable fitness benefits may be associated with the faster development of foraging skills. Young forced to leave their natal areas prior to the development of a proper foraging strategy may be subject to increased mortality risks, making rapid development of foraging mechanics of vital importance. In contrast, longer summers in Florida allow for longer post-fledging periods and time in which to develop a proper foraging strategy. Whether benefits associated with faster learning

are important during post-fledging dispersal, however, is not known, and poses an interesting question for future research.

Finally, the strong association between rates of learning and social interactions has important management implications. Osprey reintroduction programs are increasing in number and scope along the Eastern Seaboard in an effort to return ospreys to areas they once occupied. Reintroduction programs striving to maximize survival probabilities of released birds may have greater success by releasing young in clusters rather singly. At a minimum, complete broods of at least two rather than single nestlings should be taken from donor populations. Related young subsequently should be hatched from the same tower. Separating related young eliminates potential benefits associated with faster learning rates, benefits that may increase survivorship of released young and increase the likelihood that ospreys will once again be common.

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BIOGRAPHICAL SKETCH

Thomas C. Edwards, Jr., was born 21 August 1956 at Quantico, Virginia. According to his brother, Tom's interest in biology and the great outdoors was firmly encouraged by their mother, who forever banished Tom from the basement after he and his chemistry set burned up a load of laundry.

After a less than spectacular start as a collegiate at the University of California, San Diego, Tom migrated north to Humboldt State University, California, where he majored in wildlife management and trips up a nearby logging road. His interest in avian ecology was stimulated by a semester's break from classes, in which he assisted in a golden eagle research project at the Snake River Birds of Prey Research Area, near Boise, Idaho. It was here he first learned to love the Great Basin Desert and the relationship between hot weather and cold beer.

He subsequently returned to Humboldt, graduated, worked for the Bureau of Land Management in Safford, Arizona, slipped a disc and had surgery, got married, and moved to Albuquerque, New Mexico, to begin a master's degree in biology at the University of New Mexico--all in the 365 day period known as 1980.

Upon receipt of a M.S. in biology in 1983, Tom's new-found family (one son, one lazy cat, and one hyper Samoyed) ignored Horace Greeley's

advice and moved east, where they all enrolled Tom in the Ph.D. program in wildlife ecology at the University of Florida. After a series of events remarkably similar to those outlined in Pee Wee's Great Adventure, Tom finally received a Ph.D. degree with a specialization in wildlife ecology in May 1987.

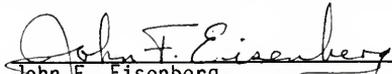
He undoubtedly would have taken a year longer to write his dissertation and graduate if it wasn't so humid in Florida.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



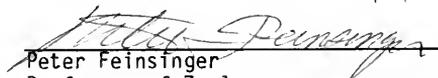
Michael W. Collopy, Chairman
Associate Professor of Forest
Resources and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



John F. Eisenberg
Kathryn Ordway Professor of
Ecosystem Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



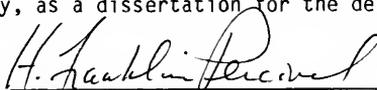
Peter Feinsinger
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Stephen R. Humphrey
Associate Professor of Forest
Resources and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



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This dissertation was submitted to the Graduate Faculty of the School of Forest Resources and Conservation in the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May 1987

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