

## SIMILARITY IN THE DEVELOPMENT OF FORAGING MECHANICS AMONG SIBLING OSPREYS<sup>1</sup>

THOMAS C. EDWARDS, JR.<sup>2</sup>

Florida Cooperative Fish and Wildlife Research Unit, Department of Wildlife and Range Sciences, University of Florida, Gainesville, FL 32611

**Abstract.** The development of foraging behavior was examined in a population of fledgling Ospreys (*Pandion haliaetus*) in north-central Florida during the 1985 and 1986 post-fledging periods. Related young (siblings) foraged together throughout much of the post-fledging period while young from single chick nests ("singletons") foraged by themselves. Related young had greater capture success over time relative to singleton birds and did not differ statistically from one another. Individual young in both years exhibited considerable variability in foraging technique, although related young had similar foraging techniques. The possible role of socially facilitated learning in enhancing the development of foraging skills in fledgling Ospreys is discussed.

**Key words:** Foraging mechanics; Osprey; *Pandion haliaetus*; social facilitation; capture success; Florida.

### INTRODUCTION

One method by which naive birds are thought to learn appropriate foraging behaviors is simple trial and error (Kamil and Yoerg 1982). Through repeated sampling of their environment, young eventually learn to recognize cues associated with successful foraging bouts while cues associated with unsuccessful bouts are ignored. Another method thought to aid in the development of foraging behaviors is "social facilitation" (Thorpe 1963), whereby naive young learn appropriate behaviors by observing more experienced "models." Here young learn not only through individual trial and error, but also by observing and incorporating into their behavioral repertoire successful foraging behaviors exhibited by the model(s). Little is known, however, of the effect interacting juveniles have on the development of each other's foraging behavior.

Here, I examine the ontogeny of foraging behaviors in fledgling Ospreys (*Pandion haliaetus*) in north-central Florida in light of potential benefits derived from interactions with other fledgling Ospreys. Several aspects of Osprey post-fledging behavior make them ideal study

organisms for field studies of this nature. First, young segregate from adults early in the post-fledging period, and interactions with adults are restricted to periods when prey is transferred. Young rarely follow adults during foraging flights and appear capable of developing successful foraging behaviors in the absence of adults (see Schaadt and Ryman 1982). Thus, the ontogeny of foraging behaviors in naive young bereft of experienced adult models may be observed. Second, related young (siblings) typically remain together once they fledge (Beebe 1974, Stinson 1977, Edwards 1987), thereby providing opportunity to observe developmental aspects of foraging among related young and contrast this development with that exhibited by singleton young.

Two aspects of the ontogeny of foraging behaviors in Ospreys are explored. I first examine whether individual young exhibit differences in foraging behaviors (Van Valen 1965, Curio 1976, Chesson 1984), or whether certain foraging techniques are so important that all young eventually converge in behavior. Alternatively, study of individual foraging behaviors might indicate that individuals using different foraging techniques can each be a successful forager (e.g., Wunderle and Lodge 1988). I next examine whether foraging behaviors develop at similar rates among young Ospreys. While foraging behavior develops in part through a trial and error process (Kamil and Yoerg 1982), the rate of development may be affected by social interactions with con-

<sup>1</sup> Received 7 March 1988. Final acceptance 25 August 1988.

<sup>2</sup> Present address: U.S. Fish and Wildlife Service, Utah Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322-5210.

specifics (Turner 1964, Dawson and Foss 1965, Cronhelm 1970, Sasvári 1979, but see Klopfer 1959).

#### STUDY AREA AND METHODS

I conducted my research on Newnan's Lake, Alachua County, Florida, from April to September 1985 and 1986. Newnan's Lake, located 15 km east of Gainesville, Florida, is a 2,400-ha hypereutrophic 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 nest trees and marked singleton and related nestling Ospreys with unique color-band combinations prior to fledging. Data on the foraging behavior of individual young were collected from a boat anchored offshore at locations that facilitated simultaneous observation of several birds. Because of difficulties associated with maintaining continuous observation of the same individual, individuals were watched only until the completion of a 15-min period or until a successful capture of prey was made. Instances where I was unable to identify individuals were excluded from analysis. Behavioral observations were collected during two 10-day periods each month and were placed in five 30-day categories (i.e., 30 days contained observations from approximately 15–45 days postfledging,  $60 \pm 15$  days,  $90 \pm 15$  days,  $120 \pm 15$  days, and  $150 \pm 15$  days). I considered young to have fledged once they left the nest tree.

A capture attempt included any stooping effort that brought the bird within 3 m of the water surface. I defined a successful capture as the capture and retention of a prey item for at least 15 sec or until the bird landed in a tree to begin feeding. Loss of prey items within the first 15 sec was due primarily to pirating attempts by other birds or the inability of the bird to grasp and control the fish. Multiple attempts for the same prey item each constituted one capture attempt.

For each successful and unsuccessful foraging bout I determined water reflectance (glare), foraging height, and flight direction of the bird relative to wind. A light meter was used to estimate glare. Measurements were taken facing the same direction as the foraging bird to mimic as closely

as possible the conditions faced by the bird. Bird foraging height was estimated from triangulation using a range finder to estimate distance and a clinometer to estimate horizontal angle. Foraging heights were placed into 0- to 3-, 4- to 6-, 7- to 9-, 10- to 12-, and 13- to 15-m categories, and the midpoint of each used for analysis. Direction of flight was subtracted from wind direction as a measure of flight relative to wind. Angles to the left of directly into the wind were treated as negatives.

A repeated measures analysis (Sokal and Rohlf 1981) of successful captures weighted by the number of attempts was used to examine whether capture success of individual young differed with respect to time and to other young. Individual Ospreys were considered random effects; time was treated as a fixed effect. Because weighted captures can be considered "counts," data from each year were fitted to main-effects log-linear models (Feinberg 1980, Agresti 1984). Lambda estimates ( $\pm$ SE), which represent the difference between expected and observed values (i.e., cell residuals; Agresti 1984), were calculated for each cell in the model and used to test for differences between fledglings. For example, a positive lambda estimate with respect to capture success indicates that the average success of a particular fledgling was greater than that of other fledglings. Whether two fledglings differed significantly was determined by comparing the  $z$ -score,

$$z = (a_1 - a_2) / [\text{SE}_1^2 + \text{SE}_2^2 - 2 \times \text{cov}(a_1, a_2)]^{1/2}$$

where  $a_1$ ,  $\text{SE}_1$  and  $a_2$ ,  $\text{SE}_2$  are the lambda estimates and their SEs for fledglings 1 and 2, respectively, and  $\text{cov}(a_1, a_2)$  is the covariance between fledglings 1 and 2, to the desired level of significance.

To test whether young differed with respect to technique I examined pooled and individual likelihood ratios ( $G^2$ ) of logistic models (Agresti 1984) describing relationships between capture success and the measured environmental parameters. The procedure is analogous to analysis of covariance and first determines whether the logistic models describing individual foraging technique are homogeneous. Presence of significant heterogeneity among the models would indicate that young differed from one another with respect to foraging technique. Nonsignificant pooled  $G^2$ s would imply similarity in technique among young.

TABLE 1. Percent capture success (attempts) for individual fledgling Ospreys in relation to days from fledging, 1985 and 1986. Note positive direction of lambda estimates for related young indicating greater average capture success relative to singleton young.

Year/bird <sup>a</sup>	Days from fledging					Lambda estimate <sup>b</sup>	SE
	30	60	90	120	150		
<b>1985</b>							
A	18.1 (83)	24.4 (86)	35.3 (34)	— <sup>c</sup>	58.6 (29)	-0.155	0.074
B1	23.1 (78)	29.9 (87)	55.6 (27)	66.7 (24)	66.7 (21)	0.111	0.062
B2	25.0 (64)	31.9 (69)	56.3 (16)	68.4 (19)	61.3 (31)	0.115	0.062
C1	18.1 (72)	39.6 (53)	59.0 (39)	69.6 (23)	72.0 (25)	0.170**	0.060
C2	19.0 (42)	34.6 (26)	59.1 (22)	73.1 (26)	67.6 (37)	0.154*	0.060
D	27.9 (61)	22.9 (109)	32.2 (59)	— <sup>c</sup>	— <sup>c</sup>	-0.161	0.101
E	23.3 (43)	29.8 (57)	32.9 (79)	45.7 (46)	57.9 (19)	-0.131	0.068
F	17.6 (51)	29.8 (47)	— <sup>c</sup>	48.7 (39)	57.1 (28)	-0.102	0.076
Mean (SE)	21.5 (1.4)	30.4 (1.9)	47.2 (4.9)	62.0 (4.8)	63.0 (2.2)		
<b>1986</b>							
A	19.0 (84)	39.3 (56)	37.8 (45)	54.5 (33)	62.9(35)	0.011	0.064
B	21.1 (71)	27.0 (37)	29.9 (77)	52.9 (34)	62.1 (29)	-0.086	0.069
C	27.3 (33)	26.8 (56)	30.9 (68)	— <sup>c</sup>	— <sup>c</sup>	-0.089	0.104
D1	22.9 (48)	36.8 (38)	58.8 (17)	72.2 (18)	68.4 (19)	0.201***	0.061
D2	22.0 (50)	37.3 (59)	57.9 (19)	66.7 (30)	68.2 (22)	0.185**	0.061
E	20.9 (67)	26.0 (73)	31.9 (47)	50.0 (36)	57.1 (28)	-0.117*	0.070
F1	— <sup>c</sup>	32.1 (56)	55.2 (29)	64.7 (34)	66.7 (30)	0.150**	0.066
F2	25.0 (36)	— <sup>c</sup>	58.3 (12)	70.0 (20)	65.5 (29)	0.181	0.066
G	26.2 (42)	26.1 (46)	32.1 (78)	56.7 (30)	54.8 (31)	-0.181	0.069
H	18.2 (44)	27.8 (36)	35.1 (37)	51.2 (43)	54.3 (35)	-0.117	0.069
I	16.0 (75)	29.0 (69)	34.0 (53)	48.4 (31)	58.3 (36)	-0.123	0.071
J	27.1 (70)	29.8 (57)	34.5 (29)	57.7 (26)	60.0 (30)	-0.012	0.066
K	20.0 (55)	29.8 (57)	32.7 (52)	54.5 (33)	61.9 (21)	-0.061	0.064
L	26.3 (38)	28.8 (52)	34.5 (29)	— <sup>c</sup>	— <sup>c</sup>	-0.043	0.100
Mean (SE)	22.5 (1.0)	30.5 (1.2)	40.3 (3.1)	58.3 (2.3)	61.7 (1.4)		

<sup>a</sup> Birds with same letter designation in the same year are siblings.

<sup>b</sup> From marginal totals collapsed across days from fledging.

<sup>c</sup> Insufficient captures ( $n = 5$ ) by bird observed in this time period.

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

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

## RESULTS

Behavioral data for eight color-banded young in 1985 and 14 color-banded young in 1986 were analyzed. Fledgling Ospreys attempted to capture prey as early as 5 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 postfledging.

The ability of young in both years to successfully capture prey differed significantly with respect to days from fledging (1985,  $G^2 = 194.5$ ,

$df = 4$ ,  $P < 0.001$ ; 1986,  $G^2 = 288.6$ ,  $df = 4$ ,  $P < 0.001$ ). Not unexpectedly, the mean capture success of each individual young increased with age (Table 1). Individuals in both years also differed among one another with respect to their ability to successfully capture fish throughout the postfledging period (1985,  $G^2 = 27.7$ ,  $df = 7$ ,  $P < 0.001$ ; 1986,  $G^2 = 43.2$ ,  $df = 13$ ,  $P < 0.001$ ). Difference in capture success of singleton and related young was most pronounced from 90 to 120 days postfledging. By the end of the postfledging period, however, success rates of young did not differ (1985,  $G^2 = 2.96$ ,  $df = 6$ ,  $P = 0.814$ ; 1986,  $G^2 = 4.41$ ,  $df = 11$ ,  $P = 0.956$ ).

Lambda estimates of capture success of related young were higher than those of singleton young in both years, indicating that related young made substantially more successful captures throughout the entire postfledging period than did sin-

TABLE 2. Multiple comparisons of capture success lambda estimators of each singleton young with related young during the 1985 and 1986 postfledging periods.

Bird <sup>a</sup>	1985				Bird <sup>a</sup>	1986			
	Lambda estimate	SE	Covariance with:			Lambda estimate	SE	Covariance with:	
			C1/C2	B1/B2				D1/D2	F1/F2
C1/C2* <sup>b</sup>	0.214	0.061	—	-0.0002	D1/D2*	0.218	0.061	—	-0.0002
B1/B2†	0.159	0.062	-0.0002	—	F1/F2†	0.179	0.062	-0.0002	—
F†	-0.065	0.076	-0.0006	-0.0005	A*†	0.040	0.065	-0.0002	-0.0002
E	-0.084	0.099	-0.0004	-0.0004	J*†	0.017	0.067	-0.0002	-0.0002
D†	-0.109	0.099	-0.0017	-0.0017	L*†	0.001	0.062	-0.0008	-0.0009
A	-0.115	0.078	0.0009	0.0008	K†	-0.032	0.069	-0.0002	-0.0002
					C*,†	-0.045	0.103	-0.0009	-0.0009
					G†	-0.052	0.069	-0.0002	-0.0003
					B†	-0.057	0.069	-0.0002	-0.0003
					E	-0.088	0.070	-0.0003	-0.0003
					H	-0.088	0.070	-0.0003	-0.0003
					I	-0.093	0.070	-0.0003	-0.0003

<sup>a</sup> Birds with the same letter designation in the same year are siblings.

<sup>b</sup> Singleton young with the same superscript symbol as each pair of related young (\* or †) had statistically similar ( $P > 0.0125$  in 1985;  $P > 0.005$  in 1986) success rates. Level of significance adjusted to control Type I error (Bonferroni inequality, Sokal and Rohlf 1981).

gletton young (Table 1). Siblings, however, did not differ from one another with respect to average capture success in 1985 (B1 vs. B2,  $z = -0.044$ ,  $P = 0.482$ ; C1 vs. C2,  $z = 0.182$ ,  $P = 0.572$ ) or 1986 (D1 vs. D2,  $z = 0.182$ ,  $P = 0.572$ ; F1 vs. F2,  $z = -0.322$ ,  $P = 0.374$ ). Singleton young exhibited greater variation among one another with respect to average capture success, but based on comparisons of the maximum difference in lambda estimates in each year, did not differ among one another (1985, F vs. D,  $z = 0.402$ ,  $P = 0.687$ ; 1986, A vs. I,  $z = 1.269$ ,  $P = 0.204$ ). However, because the maximum average success of a singleton bird did not differ from the minimum average success of a young with a sibling, it was not possible to consider all singleton young as a group distinct from related birds (1985, B1 vs. F,  $z = 1.600$ ,  $P = 0.109$ ; 1986, F1 vs. A,  $z = 1.471$ ,  $P = 0.141$ ). Instead, a comparison of the average capture success of each singleton young with each group of related young indicates some singleton young had significantly lower success rates than related young while others had success rates similar to related young (Table 2).

With the exceptions of bird D in 1985 (Rayleigh's test,  $F_{2,226} = 4.64$ ,  $P = 0.010$ ) and B in 1986 ( $F_{4,243} = 5.02$ ,  $P < 0.001$ ), the direction of foraging flight relative to wind was constant over time for each individual bird. Although all young tended to forage within  $\pm 20^\circ$  of directly into the wind (Table 3), there was considerable variation among individuals with respect to preferred foraging directions (Rayleigh's test: 1985,  $F_{7,1663} =$

23.48,  $P < 0.001$ ; 1986,  $F_{13,2696} = 26.84$ ,  $P < 0.001$ ). Related young in both years had similar preferred foraging directions (Rayleigh's test: 1985, B1 vs. B2,  $F_{1,434} = 0.31$ ,  $P = 0.575$ , C1 vs. C2,  $F_{1,363} = 2.41$ ,  $P = 0.121$ ; 1986, D1 vs. D2,  $F_{1,318} = 0.33$ ,  $P = 0.56$ , F1 vs. F2,  $F_{1,244} < 0.01$ ,  $P = 0.994$ ).

When differences due to age were controlled, young did not differ among one another with respect to foraging height (Cochran-Mantel-Haenszel test: 1985,  $CMH = 6.99$ ,  $df = 7$ ,  $P = 0.430$ ; 1986,  $CMH = 8.87$ ,  $df = 13$ ,  $P = 0.783$ ). Instead, differences in foraging height were related to time, with young in both years gradually increasing foraging height throughout the post-fledging period (Table 4).

The foraging technique of individual young was constant over time (Table 5). I subsequently pooled observations for each individual over time to determine the relationship that glare, direction of flight relative to wind, and foraging height, had to capture success. All young but one (1985; E) had a significant positive relationship between foraging height and capture success. Both direction of flight relative to wind and glare varied considerably with respect to the direction of their relationship to capture success, with 13 of 22 birds having a positive relationship with each variable. With the exception of two birds (1986; G and H), neither direction of flight relative to wind nor glare had significant relationships with capture success.

A test for heterogeneity in technique among

TABLE 3. Direction of foraging flights relative to wind (wind direction standardized to 0°) of individual fledgling Ospreys during the 1985 and 1986 postfledging periods.

1985				1986			
Bird*	n	Mean angle	(SD)	Bird	n	Mean angle	(SD)
A	232	353	(36)	A	253	12	(34)
B1	237	10	(37)	B	248	349	(37)
B2	199	12	(32)	C	157	13	(41)
C1	212	347	(37)	D1	140	343	(35)
C2	153	340	(35)	D2	180	346	(38)
D	229	10	(36)	E	251	14	(39)
E	244	352	(40)	F1	149	18	(31)
F	165	337	(38)	F2	97	18	(36)
				G	227	345	(31)
				H	195	353	(32)
				I	264	351	(32)
				J	212	14	(34)
				K	218	20	(35)
				L	119	7	(35)

\* Birds with same letter designation in the same year are siblings.

young of both years indicated young differed among themselves (1985,  $G^2 = 1,868.9$ ,  $df = 1,602$ ,  $P < 0.001$ ; 1986,  $G^2 = 2,885.8$ ,  $df = 2,646$ ,  $P = 0.001$ ). Thus, although individual young were consistent over time with respect to technique, young of each year differed among themselves in how the measured variables were related to capture success. Related young, however, did not differ with respect to foraging technique in 1985 (B1 vs. B2,  $G^2 = 426.8$ ,  $df = 386$ ,  $P = 0.074$ ; C1 vs. C2,  $G^2 = 291.5$ ,  $df = 313$ ,  $P = 0.803$ ) or 1986 (D1 vs. D2,  $G^2 = 221.2$ ,  $df = 278$ ,  $P = 0.995$ ; F1 vs. F2,  $G^2 = 164.9$ ,  $df = 214$ ,  $P = 0.774$ ).

## DISCUSSION

That social learning plays some role in the development of foraging mechanics in fledgling Ospreys is supported by several lines of evidence. First, capture success of young with siblings was initially greater than that exhibited by singleton young, even though young in both years had similar success rates by the end of the postfledging period. Second, although there existed differences in how Ospreys responded to environmental parameters throughout the postfledging period, related birds that foraged together had similar response patterns. Finally, the tendency for related young to remain together throughout the postfledging period provided the opportunity

TABLE 4. Mean foraging height (m) of fledgling Ospreys in relation to days from fledging.

Days from fledging	1985			1986		
	n	$\bar{x}$	(SE)	n	$\bar{x}$	(SE)
30	8	8.12	(0.11)	13	8.45	(0.08)
60	8	8.28	(0.07)	13	8.02	(0.10)
90	7	9.51	(0.25)	14	9.57	(0.17)
120	6	10.50	(0.40)	12	9.25	(0.19)
150	7	10.15	(0.23)	12	9.50	(0.21)

\* Means are based on the midpoints of each 3-m foraging height (see Methods).

for young to interact and develop similar foraging behaviors. Thus, the close association of related young throughout the postfledging period and the between-year consistency in results suggest the possibility that information may be being transferred between related young.

One possible benefit of postfledging interactions among Ospreys may be increased rates of acquisition of appropriate foraging behaviors resulting from more frequent exposure to successful foraging bouts by other young Ospreys (Turner 1964, Cronhelm 1970, but see Klopfer 1959). In fish-eating birds like Ospreys, young must integrate information such as glare (see also Carl 1987), water clarity and wind direction into a successful foraging strategy (Grubb 1977), a process that probably involves both innate and learned behaviors. For example, adjusting flight direction relative to wind as a means of decreasing energy expended for active flight is so vital a component to flight behavior that its application to foraging may be largely automatic. In contrast, use of different heights during foraging bouts, which is thought to influence the number and diversity of available prey in plunge-diving birds (Dunn 1972), may represent a more subtle foraging skill requiring greater time to develop. While both skills undoubtedly develop over time, the rate of development of the latter may be enhanced through mechanisms such as socially facilitated learning.

A key difference reported here is the apparent increased learning rate found in naive young having the opportunity for continuous interaction with other naive young throughout the postfledging period. These results are in direct contrast to the slower learning rates reported by Klopfer (1959) for naive European Greenfinches (*Car-*

TABLE 5. Parameter estimates from logistic regression analysis of the effect of foraging height, direction of flight relative to wind direction, and glare on capture success of fledgling Ospreys.

Year/ bird <sup>b</sup>	Test <sup>a</sup>			Parameter estimates (SE)					
	G <sup>2</sup>	df	P-value	Intercept	Height	Direction	Glare		
1985									
A	206.3	213	0.616	-2.583*** (0.765)	0.214*** (0.052)	0.005 (0.003)	-0.026	(0.005)	
B1	237.7	212	0.109	-1.565* (0.762)	0.172*** (0.047)	-0.004 (0.003)	-0.034	(0.049)	
B2	189.1	174	0.205	-2.690** (0.082)	0.022*** (0.005)	0.002 (0.004)	0.037	(0.053)	
C1	166.9	185	0.826	-4.095*** (0.881)	0.328*** (0.057)	0.007 (0.004)	0.071	(0.056)	
C2	124.6	128	0.569	-3.529** (1.065)	0.438*** (0.076)	0.005 (0.005)	-0.055	(0.065)	
D	224.4	213	0.283	-2.143** (0.773)	0.143** (0.052)	0.003 (0.004)	-0.012	(0.051)	
E	224.7	219	0.381	-3.968*** (0.833)	0.303 (0.052)	0.042 (0.003)	0.046	(0.054)	
F	126.1	146	0.882	-5.760*** (1.168)	0.444*** (0.082)	<0.001 (0.004)	0.093	(0.006)	
1986									
A	213.3	233	0.819	-4.081*** (0.787)	0.390*** (0.054)	0.002 (0.004)	0.003	(0.049)	
B	195.8	226	0.928	-6.375*** (0.947)	0.508** (0.068)	-0.003 (0.004)	0.066	(0.056)	
C	143.7	145	0.515	-4.506*** (1.019)	0.399*** (0.078)	-0.003 (0.004)	-0.002	(0.006)	
D1	91.7	118	0.965	-5.228*** (1.297)	0.586*** (0.101)	0.002 (0.005)	-0.003	(0.008)	
D2	129.5	160	0.963	-5.508*** (1.068)	0.603*** (0.095)	-0.005 (0.004)	-0.014	(0.064)	
E	218.9	230	0.690	-4.491*** (0.838)	0.375*** (0.057)	-0.002 (0.003)	0.026	(0.049)	
F1	108.6	133	0.940	-5.984*** (1.286)	0.679*** (0.111)	0.001 (0.005)	0.003	(0.076)	
F2	56.3	81	0.983	-5.247*** (1.443)	0.494*** (0.104)	-0.005 (0.006)	0.067	(0.082)	
G	161.3	204	0.988	-2.871*** (0.806)	0.512*** (0.074)	0.004 (0.005)	-0.209***	(0.059)	
H	139.7	175	0.977	-7.338*** (1.241)	0.570*** (0.083)	-0.001 (0.005)	0.131*	(0.066)	
I	232.9	244	0.684	-5.115*** (0.906)	0.431*** (0.061)	-0.003 (0.004)	0.032	(0.051)	
J	181.8	192	0.690	-5.231*** (0.978)	0.485*** (0.073)	0.001 (0.004)	0.027	(0.061)	
K	175.2	198	0.877	-3.186** (0.814)	0.384*** (0.062)	0.004 (0.004)	-0.085	(0.053)	
L	104.2	107	0.559	-5.929*** (1.335)	0.421*** (0.084)	-0.003 (0.006)	0.089	(0.086)	

<sup>a</sup> Ho: Foraging technique of individual bird is constant throughout postfledging.

<sup>b</sup> Birds with same letter designation in the same year are siblings.

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

*duelis chloris*) learning in the presence of other naive young. Klopfer concluded, however, that such inhibition in learning would be maladaptive in species that, in contrast to European Greenfinches, are more opportunistic feeders and exploit variable environments. Variability in the fish resource base is pronounced at Newnan's Lake (Edwards 1988: fig. 1), suggesting that inhibition in learning might not be expected to occur in this population of Ospreys. Subsequent work by Klopfer (1961) on paired and singleton Great Tits (*Parus major*), a more exploitative feeder than European Greenfinches, showed no difference in learning rates between paired and singleton young.

While Klopfer's and these results provide support for the idea that inhibition in learning should not occur in species occupying variable environments, they do not account for the increased rate of development of capture success reported here. One possible interpretation of the increased learning rates reported here is that Klopfer's ex-

periments dealt with development of aversion discrimination, whereas capture success is more a measure of the establishment of a feeding response. Less clear are the potential benefits for Ospreys associated with faster developmental rates. Because all Ospreys in this study eventually attained similar levels of capture success, benefits associated with an increased learning rate would accrue only if there existed some temporal constraint on the learning period (e.g., dispersal or migration pressures). That Ospreys with lower rates survived equally well throughout the post-fledging period suggests that there is no penalty associated with an initially slower learning rate. It may be that these differences in success rates merely reflect variability found in this population of Ospreys, and that similarity between related young is due to the tendency of interacting individuals to converge in behavior (Galef 1976).

The development by young of several different foraging techniques having roughly equivalent success rates also suggests Ospreys are flexible in

foraging technique. Because all young eventually had similar foraging success rates, it is difficult to determine whether any of the several techniques used by this population of Ospreys conferred any foraging advantage. Wunderle and Lodge (1988) also report different foraging techniques among individual Bananaquits (*Coereba flaveola*) of the same age class, with birds exhibiting different turning patterns when foraging in nectar-rich flower patches. As with Ospreys, however, differences in technique apparently had no negative impact on the foraging success of individual Bananaquits. Whether these differences are maintained throughout time, an indicator of social transmission of information (Galef 1976), or whether they represent transitory modifications in individual foraging behavior, is unknown. That a variety of techniques can each be considered "successful" suggests some benefit exists regarding flexibility in foraging behavior.

#### ACKNOWLEDGMENTS

I thank members of my doctoral research committee, M. W. Collopy, J. F. Eisenberg, P. Feinsinger, S. R. Humphrey, and H. F. Percival, for their helpful comments on this and earlier drafts. Various drafts of this manuscript also benefitted from comments provided by C. Annett, R. J. Pierotti, J. Robinson, J. A. Smallwood, J. M. Wunderle, and one anonymous reviewer. T. B. Murphy provided constant companionship in the field and aided greatly to the collection and analysis of these data. Financial and logistical support was provided by the Florida Cooperative Fish and Wildlife Research Unit, U.S. Fish and Wildlife Service, and by grants from Sigma Xi and the Hawk Mountain Sanctuary Association. This paper is contribution No. 9233 of the Journal Series, Florida Agricultural Experimental Station, Gainesville, Florida.

#### LITERATURE CITED

- AGRESTI, A. 1984. Analysis of ordinal categorical data. John Wiley and Sons, New York.
- BEEBE, F. 1974. Field studies of the Falconiformes of British Columbia. Occas. Pap. B. C. Prov. Mus. 17.
- CARL, R. A. 1987. Age-class variation in foraging techniques by Brown Pelicans. *Condor* 89:525-533.
- CHESSON, J. 1984. Variable predators and switching behavior. *Theor. Popul. Biol.* 26:1-26.
- CRONHELM, E. 1970. Perceptual factors and observational learning in the behavioural development of young chicks, p. 393-439. *In* J. H. Crook [ed.], Social behaviour in birds and mammals: essays on the social ethology of animals and man. Academic Press, New York.
- CURIO, E. 1976. The ethology of predation. Springer-Verlag, New York.
- DAWSON, B. V., AND B. M. FOSS. 1965. Observational learning in Budgerigars. *Anim. Behav.* 13:470-474.
- DIXON, W. J. 1985. BMDP statistical software. Univ. California Press, Berkeley.
- DUNN, E. K. 1972. Effect of age on the fishing ability of Sandwich Terns (*Sterna sandvicensis*). *Ibis* 114: 360-366.
- EDWARDS, T. C., JR. 1987. Temporal and social aspects of the foraging ecology of a piscivore, the Osprey (*Pandion haliaetus*). Ph.D. diss. Univ. Florida, Gainesville.
- EDWARDS, T. C., JR. 1988. Temporal variation in prey preference patterns of adult Ospreys. *Auk* 105:244-251.
- FEINBERG, S. E. 1980. The analysis of cross-classified categorical data. Massachusetts Institute Technology Press, Cambridge.
- GALEF, B. G. 1976. Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates, p. 77-100. *In* J. S. Rosenblatt, R. A. Hinde, E. Shaw, and C. Beers [eds.], Advances in the study of behavior. Vol. 6. Academic Press, New York.
- GRUBB, T. G., JR. 1977. Weather-dependent foraging in Ospreys. *Auk* 94:146-149.
- KAMIL, A. C., AND S. I. YOERG. 1982. Learning and foraging behavior, p. 325-364. *In* P.P.G. Bateson and P. H. Klopfer [eds.], Perspectives in ethology. Ontogeny. Vol. 5. Plenum Press, New York.
- KLOPPER, P. H. 1959. Social interactions in discrimination learning with special reference to feeding behavior in birds. *Behaviour* 14:282-299.
- KLOPPER, P. H. 1961. Observational learning in birds: the establishment of behavioral modes. *Behaviour* 17:71-80.
- SAS INSTITUTE. 1982. SAS user's guide: statistics. SAS Institute, Cary, NC.
- SASVARI, L. 1979. Observational learning in Great, Blue and Marsh Tits. *Anim. Behav.* 27:767-771.
- SCHAADT, C. P., AND L. M. RYMAN. 1982. Innate fishing behavior of Ospreys. *Raptor Res.* 16:61-62.
- SHANNON, E. E., AND P. L. BREZONIK. 1972. Limnological characteristics of north and central Florida lakes. *Limnol. Oceanogr.* 17:97-110.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman and Company, New York.
- SPSSX USER'S GUIDE. 1986. McGraw-Hill, New York.
- STINSON, C. H. 1977. Familial longevity in Ospreys. *Bird-Banding* 48:72-73.
- THORPE, W. H. 1963. Learning and instinct in animals. 2nd ed. Harvard Univ. Press, Cambridge.
- TURNER, R. A. 1964. Social feeding in birds. *Behaviour* 24:1-46.
- VAN VALEN, L. 1965. Morphological variation and width of ecological niche. *Am. Nat.* 99:377-390.
- WUNDERLE, J. M., AND D. J. LODGE. 1988. The effect of age and visual cues on floral patch use by Bananaquits (Aves: Emberizidae). *Anim. Behav.* 36: 44-55.