poultry and −0.89% for the Starling. Thus it appears that the relative sizes of the yolks in the three species are similarly conservative with respect to variation in egg size.

The wet weight of the albumen was highly correlated with fresh egg weight ($r = 0.92$, $P < 0.001$), and the correlation between the albumen dry weight and egg volume was similar ($r = 0.93$); the proportion of albumen in the egg was positively correlated with increasing egg weight, but not significantly ($r = 0.347$, $P = 0.06$). Variation in egg size in the Great White Pelican therefore appears to depend mainly on the amount of albumen laid down, as is also the case in the Starling (Ricklefs 1977a) and Herring Gull (*Larus argentatus*) (Parsons 1976, Condor 78: 481).

As in the Starling, variation in the lipid fraction of the yolk (between 61.5% and 69.5%) was not correlated with either yolk size or egg size, nor with the relative size of the yolk. Nevertheless, because of the positive relationship between yolk size and egg size, larger eggs contained greater absolute amounts of lipid, although in relative terms, as a result of the negative correlation between egg size and proportionate yolk size, larger eggs contained proportionately less lipid overall ($r = -0.42$, $P < 0.01$).

In order to facilitate comparison with future studies, these relationships may be expressed more conveniently as the regression coefficients of the log values of the various egg components on log fresh egg weight (Ricklefs in litt.). Thus the slope of the regression of log wet weight of yolk on log fresh egg weight was 0.53 ± 0.12; log wet weight of albumen on log fresh egg weight was 1.17 ± 0.10; and log yolk lipid weight on log fresh egg weight was 0.55 ± 0.14.

Energy per gram of fresh egg (including shell) seems commonly to be above 1.6 $\text{kcal}\cdot\text{g}^{-1}$ in precocial species and around 1.1 $\text{kcal}\cdot\text{g}^{-1}$ in altricial ones, whereas the eggs of the Brown Pelican were intermediate at 1.37 $\text{kcal}\cdot\text{g}^{-1}$ (Lawrence and Schreiber 1974, Ricklefs 1977b). The same calculation for the Great White Pelican, using constants of 9.5 $\text{kcal}\cdot\text{g}^{-1}$ for lipid and 5.65 $\text{kcal}\cdot\text{g}^{-1}$ for nonlipid dry weight, gives a value of 1.06 $\text{kcal}\cdot\text{g}^{-1}$, typical of altricial species. The difference between the two pelican species evidently derives from the proportionately greater amount of dry matter in the egg of the Brown Pelican. Whereas the egg of the Great White Pelican is twice as heavy as that of the Brown Pelican, the dry weight of the yolk is greater in the ratio of only 1.7:1 and the dry weight of the albumen is proportionately even less, in the ratio of only 1.2:1 (Lawrence and Schreiber 1974). These differences remain unexplained.

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## The Relationship Between Prey Species Ecology and Dive Success in Ospreys

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Lambert (1943) first reported on dive success of Ospreys (*Pandion haliaetus*). Since then, several studies have analyzed various physical parameters affecting Osprey foraging, including tides (Ueoka 1974) and weather variables (Grubb 1977a). The relative success of dives from hovers and interhovers (Grubb 1977b) and the dive success of adult and juvenile Ospreys in the same area (Szaro 1978) have also been investigated. The relationship between prey species and foraging success has received little attention, although Nesbitt (1974) found substantial differences in dive success in two areas with different prey.

Here I synthesize studies reporting Osprey dive success and prey species captured under natural conditions in 13 areas, as reported in the literature. Dive success (the proportion of observed dives that were successful) is used as the measure of Osprey foraging success, as it measures the relative ease of capture. It would be less influenced by prey availability than other foraging parameters, such as foraging time required per fish caught. Also, dive success is less influenced by weather conditions than other foraging parameters (Grubb 1977a).

The studies compared here were conducted in a variety of habitats, including coastal, estuarine, river, and eutrophic, mesotrophic, and oligotrophic lake environments. Water depth and clarity, prey availability and abundance, and weather conditions varied. Because all of these variables could not be monitored, and may not have been equally important, only dive success and prey species ecology were considered here.

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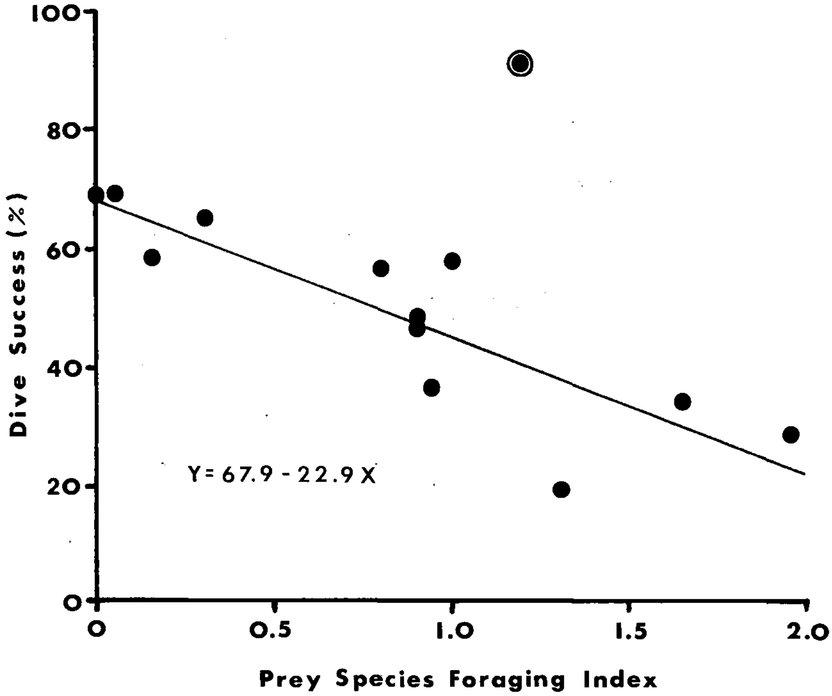

Fig. 1. Relationship of Osprey dive success and prey species foraging indices on 13 study areas. The results from Newnans Lake, Florida are circled; see text.

Dive success was determined in the same manner in these studies: by direct observation with binoculars and spotting scopes during the breeding season. The composition of prey was determined by the analysis of prey remains at nests and feeding perches [Garber 1972, MacCarter 1972, Nordbakke 1974, Szaro 1978, Swenson 1978 (at Yellowstone Lake)], or by identifying the fish at capture [French 1972, Nesbitt 1974, Ueoka 1974, Lind 1976, Grubb 1977a, Prévost 1977, Swenson 1978 (at Yellowstone River)].

To quantify the relationship between dive success and ecology of the prey, a "prey species foraging index" was calculated for the Osprey diet in each area. This index grouped fish into three broad categories according to foraging behavior: fish that feed primarily upon benthic organisms (a score of 0); fish that feed on limnetic organisms, excluding fish (1); and piscivorous fishes (2). Both obligate and facultative piscivores were included in the final category. The proportion of each prey species was multiplied by the foraging score, and the scores were added for all the prey species taken in each area. The resulting index could vary from 0.0 (only benthic-feeding fishes captured) to 2.0 (only piscivorous fishes captured). In the above calculations, the species composition of "unidentified fishes" in each study was considered to be identical to the composition of the identified portion of the diet. It was recognized that Osprey dive success in each area was the composite of possibly different rates of dive success for each prey species taken in that area.

It appeared from the results of the 13 studies that benthic-feeding fishes were most easily captured, and that piscivorous fishes were most difficult to capture (Table 1). The correlation between Osprey dive success and the prey species foraging indices (Fig. 1) was statistically significant ($r = -0.58$, df = 10, $t = -2.37, P < 0.05$). Only the Newnans Lake data deviated to a great degree from the correlation in Fig. 1. These data may represent a special case, because many dead and moribund shad were observed at the lake. These shad die after spawning (Nesbitt pers. comm.), and although Nesbitt (1974) disregarded captures of dead fish in his calculations, the moribund shad were probably especially vulnerable to Osprey predation. Therefore, these data are probably biased. If the data from Newnans Lake were excluded, the correlation would be improved ($r = -0.86$, df = 9, $t = -5.338$, $P < 0.01$).

The prey species foraging indices accounted for about 74% ($r^2$) of the observed variation in dive success (excluding Newnans Lake). Apparently, the foraging behavior of the prey species was an important factor in determining Osprey dive success.

TABLE 1. Summary of the results of 13 studies of Osprey prey species and dive success.

| Area | Reference | Dive success (%) | Prey species foraging index | Major prey species[a] | Foraging score[b] | Proportion in diet (%) | Reference for foraging score |
|---|---|---|---|---|---|---|---|
| Newnans Lake, Florida | Nesbitt (1974) | 91 (29)[c] | 1.20 | Gizzard shad (*Dorosoma cepedianum*) | 1 | 73 | Walden (1964) |
| | | | | Threadfin shad (*D. petenense*) | 1 | | |
| | | | | Sunfish (*Lepomis* sp.) | 2 | 15 | Brown (1971) |
| | | | | Black crappie (*Pomoxis nigromaculatus*) | 2 | | |
| | | | | Large-mouth bass (*Micropterus salmoides*) | 2 | | |
| | | | | Unidentified | | 12 | |
| Mouth of Usal Creek, California | French (1972) | 69 (144) | 0.0 | Surf smelt (*Hypomesus pretiosus*) | 0[d] | 98 | Fitch (1949) |
| | | | | Night smelt (*Spirinchus starksi*) | 0[d] | | |
| Antigonish Harbour, Nova Scotia | Prévost (1977) | 69 (2,268) | 0.05 | Winter flounder (*Pseudopleuronectus americanus*) | 0 | 90+ | Lagler et al. (1962) |
| Flathead Lake, Montana | MacCarter (1972) | 65 (202) | 0.30 | Largescale sucker (*Catostomus machrocheilus*) | 0 | 59 | Brown (1971) |
| | | | | Whitefish (*Prosopium* sp.) | 1 | 26 | Brown (1971) |
| | | | | Unidentified | | 11 | |
| Humboldt Bay, California | Ueoka (1974) | 58 (1,660) | 0.15 | Surfperch (Embiotocidae) | 0 | 64 | De Martini (1969) |
| | | | | Unidentified | | 27 | |
| Craine Prairie Reservoir, Oregon | Lind (1976) | 58 (60) | 1.00 | Salmonidae | 1 | 57 | Brown (1971) |
| | | | | Tui chub (*Siphateles bicolor*) | 1 | 43 | Kimsey (1954) |
| Eagle Lake, California | Garber (1972) | 56 (36) | 0.80 | Tui chub | 1 | 48 | |
| | | | | Rainbow trout (*Salmo gairdneri*) | 1 | 34 | Brown (1971) |
| | | | | Tahoe sucker (*Catostomus tahoensis*) | 0 | 18 | |
| Yellowstone River, Wyoming | Swenson (1978) | 48 (33) | 0.90 | Cutthroat trout (*Salmo clarki*) | 1 | 90 | Brown (1971) |
| | | | | Longnose sucker (*Catostomus catostomus*) | 0 | 10 | Brown (1971) |
| Yellowstone Lake, Wyoming | Swenson (1978) | 47 (153) | 0.90 | Cutthroat trout | 1 | 88 | |
| | | | | Longnose sucker | 0 | 7 | |
| | | | | Unidentified | | 5 | |

TABLE 1. Continued.

| Area | Reference | Dive success (%) | Prey species foraging index | Major prey species[a] | Foraging score[b] | Proportion in diet (%) | Reference for foraging score |
|---|---|---|---|---|---|---|---|
| Lake George, Florida | Grubb (1977a) | 36 (283) | 0.95 | Mullet (*Mullus barbatus*) | 0 | 52 | Randall (1968) |
| | | | | Crappie (*Pomoxis* sp.) | 2 | 48 | |
| Iddefjord, Norway | Nordbakke (1974) | 34 (116) | 1.65 | Orfe (*Leuciscus idus*) | 2 | 32 | Muus (1967) |
| | | | | Northern pike (*Esox lucius*) | 2 | 25 | Muus (1967) |
| | | | | Perch (*Perca fluviatilis*) | 2 | 16 | Muus (1967) |
| | | | | Dace (*Leuciscus leuciscus*) | 1 | 8 | Muus (1967) |
| Paynes Prairie, Florida | Nesbitt (1974, pers. comm.) | 28 (50[e]) | 1.95 | Sunfish | 2 | 95 | |
| Seahorse Key, Florida | Szaro (1978) | 19 (124) | 1.30 | Speckled trout (*Cynoscion nebulosus*) | 2 | 64 | Randall (1968) |
| | | | | Striped mullet (*Mugil cephalus*) | 0 | 27 | Randall (1968) |
| | | | | Sea catfish (*Galeichthys felis*) | 0 | 8 | |

[a] Excluding species comprising less than 5%.

[b] 0 = benthic, 1 = limnetic nonpiscivorous, 2 = limnetic piscivorous.

[c] Sample size.

[d] Spawning in very shallow surf.

[e] Estimate, original data lost in fire.

Benthic-feeding fishes appeared to be more vulnerable than limnetic-feeding fishes to Osprey attack. Morphological and behavioral adaptations related to procuring food from the bottom may limit the ability of benthic-feeding fishes to perceive attack from above. Their attention may be concentrated on the bottom to a greater degree than fishes not dependent on benthic food. Piscivorous fishes, due to their predatory habits, may be comparatively swifter than nonpiscivorous, limnetic fishes. This suggests that Ospreys may select benthic fishes over other fishes when they are equally available, because they are comparatively easier to capture, but Ospreys are obviously adaptable and do not require them.

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