

AGE-CLASS VARIATION IN FORAGING TECHNIQUES BY BROWN PELICANS¹

ROBERT A. CARL²

Department of Zoology, University of Oklahoma, Norman, OK 73019

Abstract. To explore age-class variation in Brown Pelican (*Pelecanus occidentalis*) hunting success, three behavioral aspects of foraging (dive height, dive angle, and head orientation) were examined in detail. Adults had greater foraging success than birds in three younger age classes. Success improved linearly with age, but was generally lower than reported in previous studies. Both dive height and dive angle varied significantly as a function of age. Adult mean dive height was higher than that of juveniles and first-year birds, but did not differ from that of subadults. Adults, subadults, and juveniles relied more on steep dive angles and less on flat dive angles than first-year birds. Results indicated a significant positive correlation between dive height and dive angle, suggesting that refraction is important when birds are hunting prey that are relatively deep in the water. Pelicans appeared to minimize surface glare by orientating away from the sun while diving.

Key words: Brown Pelican; *Pelecanus occidentalis*; foraging; differential age-class foraging; Florida.

INTRODUCTION

In various bird species a high degree of skill is necessary to master foraging techniques, which often differ among age classes (Recher and Recher 1969, Groves 1978, Goss-Custard and Durell 1983, MacLean 1986). This phenomenon, known as differential age-class foraging, is widespread in pelagic birds (Orians 1969, Dunn 1972, Buckley and Buckley 1974, Brandt 1984). Young birds learn foraging techniques and, in the case of some pelagic birds, it is 2 to 3 years before adult levels of proficiency are attained (MacLean 1986). Our understanding of differential age-class foraging is based mainly on correlations between plumage indicators of age and various measures of foraging success (Morrison et al. 1978, Burger 1980, Greig et al. 1983); current evidence shows that foraging success improves with age in most seabirds (see review in Brandt 1984).

Plunge-divers develop highly skilled foraging techniques. In this practice, a bird must contend with surface glare, refraction, and other environmental variables in addition to the evasive tactics of the prey. Dunn (1972) observed that young Sandwich Terns (*Sterna sandvicensis*) caught prey less often than older birds. The greatest difference

in foraging success occurred on days when older Sandwich Terns dove from significantly greater heights than younger birds. Similarly, Buckley and Buckley (1974) suggested that adult Royal Terns (*S. maxima*) dove from greater heights than juvenile terns. Adult terns also dropped fewer prey and dove more often at a perpendicular angle than did juvenile terns.

Brown Pelicans (*Pelecanus occidentalis*) are the only plunge-diving member of the family Pelecanidae. Several studies have shown that adult Brown Pelicans are more successful than juveniles at catching fish (Orians 1969, Schreiber et al. 1975, Schnell et al. 1983, Brandt 1984), but the reasons for this greater adult success remain unclear. Prey-handling skills are commonly presumed to account for differences in Brown Pelican foraging success (Orians 1969). Schnell et al. (1983) indicated that gull kleptoparasitism on foraging pelicans affects success, while Brandt (1984) suggested that superior recognition of profitable food patches may influence foraging success.

The details of Brown Pelican diving techniques have received little attention. Coblenz (1986) found that, relative to juveniles, adults more often wheeled in flight preceding a dive and then resumed searching. He indicated that this may reflect a pre-dive assessment of the probability of success by adult pelicans. Allen (1923) and Orians (1969) suggested that adult pelicans dove from greater heights than juveniles, al-

¹ Received 23 July 1986. Final acceptance 9 January 1987.

² Present address: 708 E. 20th, Farmington, NM 87401.

though neither conducted a quantitative assessment of such differences.

In addition, dive angle and head orientation may play an important role in enhancing visual tracking by plunge-divers. Birds must compensate for reflected light (glare) from the surface and refracted light at the air-water interface. Refraction is reduced as the angle of view approaches perpendicular to the surface (Sustare 1979, Heuvelen 1982). Reflection should be less problematic for plunge-divers early and late in the day, when the source of light (sun) is at a low angle and can be kept to the observer's back (Lythgoe 1979). Dive height may affect the depth in the water column a plunge-diver can reach (and effectively hunt) and may influence the number and diversity of potential prey (Dunn 1972).

My study examined differences in plunge-diving by Brown Pelicans that might explain reasons for variation in age-class success. I present data on three behavioral aspects of foraging (dive angle, dive height, and head orientation) by pelicans of four age classes.

METHODS

I studied Brown Pelican foraging in August 1985 and March 1986 at South Jetty Park, Port Canaveral, Florida (28°24'N, 80°37'W). As many as 100 Brown Pelicans loafed on a beach north of the channel and fed on fish (mostly mullet, family Mugilidae; and menhaden, family Clupeidae) that schooled in the deep water of the channel (average depth = 11.3 m). My study area included the middle reach of the channel and adjacent south-beach area of the Port Canaveral harbor. The channel area is sheltered from the wind by rock jetties that provided an area of consistently calm water even on windy days.

A total of 970 dives were scored in August 1985. Observations of dives were made from land with 10 × 40 binoculars, and from a distance of less than 300 m. Pelicans were classified into the following four age-class categories, according to plumage descriptions of Bent (1922), Palmer (1962), and R. W. Schreiber (pers. comm.): (1) first-year birds (<12 months) with a white belly and uniform light-gray head feathers; (2) juveniles (12 to <22 months) with a brown-gray mottled head and neck, a blue-gray bill, and a gray-brown belly; (3) subadults (22 to <40 months) with an overall mottled brown head

and body; (4) adults (>36 months) with a black belly, and a brown and white neck.

The outcome of each pelican dive was scored using the success criterion of Orians (1969) and Schreiber et al. (1975)—a head toss after surfacing (indicative of swallowing). Unsuccessful birds rapidly drain water from their bill and do not use head-tossing motions.

As the bird entered the water I recorded dive angle as the angle of the pelican's head/bill axis relative to the water's surface. These angles were measured by sighting through a clear protractor. Dives were grouped into dive-angle categories of 0 to <10°, 10 to <20°, etc., and midpoints of each category (i.e., 5°, 15°, etc.) were used in the analyses.

I visually estimated pelican dive heights using the bird's wing span as a guide (average wingspan about 2.0 m; Palmer 1962). Dive heights were recorded as the distance above the water (in meters) from which the bird initiated its downward plunge. Dives were assigned to one of the following height categories: less than 2 m; 2 to <6 m; 6 to <12 m; and 12 to <18 m. No dives from 18 m or higher were observed. The midpoints of each dive height category were used in the analyses.

Dive outcomes and dive heights were tested for differences among age classes using a one-way analysis of variance (ANOVA, SAS Institute 1985). Mean dive height and percent success for each age class were compared using a Duncan's multiple range test (Freund and Littell 1981). Dive-height frequencies were further compared among age classes with a row-by-column multiway *G*-test (BIOM, Rohlf 1982). Dive-angle frequencies were also compared, among age classes, using the *G*-test. For row-by-column tests of dive angles versus age, dives between 30° and 60° were pooled because of the small number of dives attempted using these angles. Association between dive heights and dive angles was assessed by calculating a Pearson's product-moment correlation coefficient (*r*, Sokal and Rohlf 1981).

To explore the possible influence of sun position and glare, I recorded additional details for 41 dives in March 1986. I noted the compass bearing of the pelican's head as the bird entered the water, as well as the time (to the nearest 5 min) when the dive took place. Light-meter readings were taken every hour from 07:00 to 18:00,

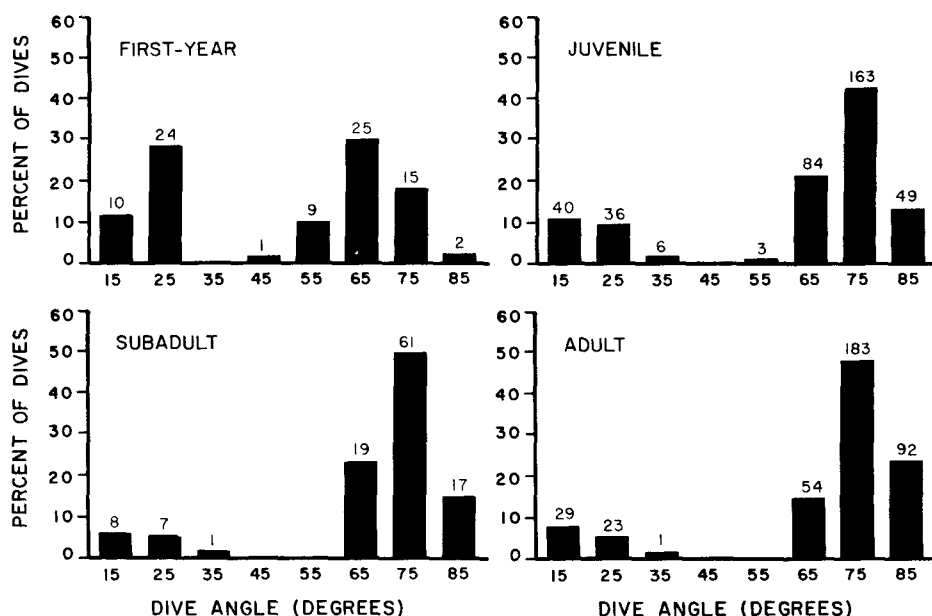


FIGURE 1. Age-class comparison of dive-angle frequencies for Brown Pelicans. Dive angles (in degrees), with midpoints of each category on abscissa. Numbers above the bars represent sample sizes.

based on local solar time (List 1961), with a photometer (Li-Cor Quantum model Li-185B). Readings were taken 1.5 m from the water's surface in units of Lux. I made 10 readings (5°, 15°, . . . , 85°, plus ambient light) at three directions—directly toward the sun, directly away from the sun, and perpendicular to the sun. The sun's position was located using sunpath-plot diagrams (McCluney 1985) along with altitude and azimuth tables (List 1961) for the Port Canaveral area.

The additional data collected in March 1986 were analyzed as follows. Light-meter readings were tested for variation related to time of day and percent cloud cover (ANOVA, SAS Institute 1985). Orientation frequencies were plotted in relation to sun position and wind direction. Sun position is indicated as 0° and wind direction as 0° (e.g., a pelican with its bill oriented directly at the sun or into the wind would be recorded as oriented at 0°). Wind data were collected hourly by weather station personnel at Patrick Air Force Base, Florida.

RESULTS

There was a significant difference among age classes for dive success ($F_{3,966} = 4.58, P < 0.01$).

Overall, adults were more frequently successful (14.4%, $n = 382$) than subadults (11.6%, $n = 121$), juveniles (7.9%, $n = 381$), or first-year birds (3.5%, $n = 86$). When these percentages were compared two groups were formed: (1) adults, subadults, and juveniles; and (2) juveniles and first-year birds.

Dives tended to be either "steep" (>60°) or "flat" (<30°). Few dives (2.2%) were between 30° and 60°. Dive angles varied as a function of age class ($G = 120.09, P < 0.01, df = 15$; see Table 1). In tests of differences in dive angle among groups, I found that dive-angles of first-year birds were significantly different from those of all other age classes. No significant difference was demonstrated between dive angles of juveniles and subadults or between subadults and adults. Statistical heterogeneity existed, however, when considering the three groups (juveniles, subadults, and adults) simultaneously. Adults, subadults, and juveniles more often made "steep" dives with angles closer to vertical than did first-year birds (Fig. 1). These older birds also made fewer "flat" dives than first-year birds.

Dive heights varied as a function of age class ($F_{3,966} = 26.77, P < 0.001$). First-year pelicans dove from an average height of 4.9 m, juveniles

TABLE 1. Number of dives attempted at various dive heights and angles (percent of dives for each dive height in parentheses).

Dive height (m)	Dive angle								Total
	15°	25°	35°	45°	55°	65°	75°	85°	
First-year (<i>n</i> = 86)									
1	7 (77.7)	2 (22.3)	—	—	—	—	—	—	9 (100)
4	3 (5.2)	21 (36.2)	—	1 (1.6)	9 (15.5)	18 (31.0)	4 (6.9)	2 (3.4)	58 (100)
9	—	1 (5.9)	—	—	—	—	9 (52.9)	7 (41.20)	17 (100)
15	—	—	—	—	—	—	2 (100)	—	2 (100)
Juvenile (<i>n</i> = 381)									
1	34 (89.5)	2 (5.3)	—	—	—	2 (5.3)	—	—	38 (100)
4	6 (5.4)	33 (30.0)	5 (4.5)	—	—	44 (40.0)	19 (17.3)	3 (2.7)	110 (100)
9	—	—	1 (0.6)	—	3 (1.8)	38 (22.7)	109 (65.3)	16 (9.6)	167 (100)
15	—	1 (1.5)	—	—	—	—	35 (53.0)	30 (45.4)	66 (100)
Subadult (<i>n</i> = 121)									
1	4 (100)	—	—	—	—	—	—	—	4 (100)
4	4 (12.5)	6 (18.8)	—	—	—	15 (46.9)	4 (12.5)	3 (9.4)	32 (100)
9	—	3 (1.8)	1 (1.8)	—	—	8 (14.5)	38 (69.1)	7 (12.7)	55 (100)
15	—	—	—	—	—	—	19 (63.3)	11 (36.7)	30 (100)
Adult (<i>n</i> = 382)									
1	19 (82.6)	3 (13.0)	—	—	—	1 (4.3)	—	—	23 (100)
4	10 (11.7)	19 (22.4)	1 (1.2)	—	—	31 (36.5)	20 (23.5)	4 (4.7)	85 (100)
9	—	1 (0.6)	—	—	—	21 (13.5)	114 (73.1)	20 (12.8)	156 (100)
15	—	—	—	—	—	1 (0.8)	49 (41.5)	68 (57.6)	118 (100)
Total	89	90	8	1	12	186	422	164	970

from 7.8 m, subadults from 8.9 m, and adults from 9.3 m. When dive height means were compared three groups were formed: (1) adults and subadults; (2) juveniles; and (3) first-year birds. Tests of dive height among groups indicated that first-year birds dove from heights significantly different from older age classes ($G = 100.5$, $P < 0.01$, $df = 9$). When the three older groups (juveniles, subadults, and adults) were considered simultaneously, significant differences were found. Adults and subadults made more dives from heights over 12 m than juveniles and first-year birds. Adults, subadults, and juveniles made more dives from heights 6 to 12 m than did first-year birds. First-year birds made more dives from heights 2 to 6 m than juveniles, subadults, and adults. Adults and subadults made fewer dives from low heights (<2 m) than juveniles and first-year birds (Fig. 2).

Success appeared to vary as a function of dive angle and dive height, although samples were too small for statistical comparison. Dives from more vertical angles (>60°) were more productive than dives from all other angles (Table 2). Only one successful dive between 30° and 60° was recorded. This may represent a range of dive angles

where there are unacceptable tradeoffs between dive height and refraction. Success was low for all birds using angles less than 30°. Dive height at which success was greatest varied among age classes (Table 3). Adults were consistently successful across a wide range of heights (up to 18 m), whereas first-year birds were most successful from 2 to 6 m, and juveniles and subadults were most successful from 6 to 12 m. Adults were more successful than all other age classes diving from 12 up to 18 m. Success was lowest for all birds from heights less than 2 m.

There was a significant positive correlation ($r = 0.72$, $P < 0.001$, $n = 970$) of dive height and dive angle. As dive heights increased, dive angles approached vertical (Table 1).

Light reflected from the surface varied as a function of time ($F_{15,362} = 6.86$, $P < 0.001$). As expected, on clear days there was greater reflectance when taking measurements in the direction of the sun, compared to those obtained perpendicular or directly away from the sun. Reflected light also varied significantly between sunny and cloudy days for measurements taken: (1) directly toward the sun ($F_{1,70} = 23.00$, $P < 0.001$); (2) perpendicular to sun ($F_{1,70} = 11.78$, $P < 0.001$);

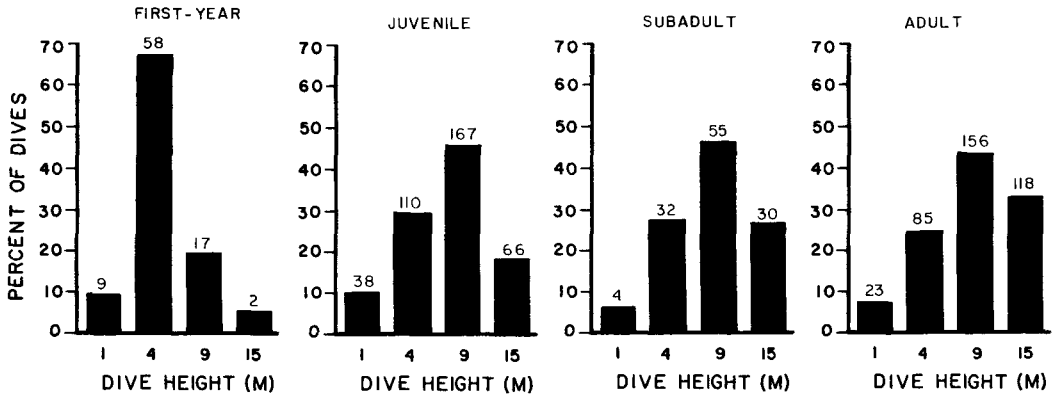


FIGURE 2. Age-class comparison of dive-height frequencies for Brown Pelicans. Dive heights (m), with midpoints of each category on abscissa. Numbers above the bars represent sample sizes.

and (3) directly away from the sun ($F_{1,70} = 4.36$, $P < 0.05$). Generally, reflectance was lower early in the morning and late in the afternoon. On cloudy days, the greatest reflectance was found from about 11:00 to 13:00 (Solar Time), while on clear days, reflectance was relatively high throughout most of the day.

Pelicans showed a preference for orientating away from the sun and wind when diving. The mean angle of pelican head orientation relative to the sun's position was 135.6° ($SD = 36.1^\circ$; Fig. 3A). The modal bearing was 150° . Similarly, the mean angle of pelican head orientation relative to wind direction was 127.3° ($SD = 41.1^\circ$), with the mode again being 150° (Fig. 3B). The average wind speed during these observations was 13.6 knots (7.0 m/sec), with gusts to 19.1 knots (9.8 m/sec).

DISCUSSION

The adult pelicans in this study had higher foraging success than the birds of other age classes. Success improved linearly with age, but it was generally lower than has been reported previously (Orians 1969, Schnell et al. 1983, Brandt 1984). This difference between studies may have been due to prey size and hunting conditions. Pelicans in my study fed in deeper water and on larger prey than noted in the investigations by Schnell et al. (1983) and Brandt (1984). Hunting large prey may have reduced diving success but increased yield per catch. Pelicans also supplemented their diet by feeding on offal thrown from commercial fishing boats. Schreiber et al. (1975) suggested that hunger may affect the diving process. Pelicans that rely partially on scavenging

may develop diving skills more slowly than pelicans that plunge-dive exclusively. Prey density may affect foraging success (Brandt 1984), but that was not measured during this study.

Dive angle varied significantly as a function of age. First-year birds used "steep" dive angles (more than 60°) and "flat" dive angles (less than 30°) almost equally, while juveniles used steep angles for 77.7%, subadults 86.7%, and adults 85.1% of their dives. Dive angle influences the amount of refraction encountered by a pelican. As dive angles approach the horizontal, the difference between the dive angle and refracted angle increases (Fig. 4). This "refractive error" is caused by the reduction in the speed of light as it enters a denser medium (water) and can be calculated using a variation of Snell's Law (Huevelen 1982):

$$n_1 \sin(90^\circ - \theta_1) = n_2 \sin(90^\circ - \theta_2),$$

TABLE 2. Comparison among age classes of 102 successful dives as a function of dive angle.

Dive angle	Age class*			
	First-year	Juvenile	Subadult	Adult
15°	—	—	2 (14.3)	6 (10.9)
25°	1 (33.3)	6 (20.0)	—	5 (9.1)
35°	—	1 (3.3)	—	—
45°	—	—	—	—
55°	—	—	—	—
65°	1 (33.3)	6 (20.0)	5 (35.7)	11 (20.0)
75°	1 (33.3)	11 (36.7)	4 (28.6)	18 (32.7)
85°	—	6 (20.0)	3 (21.4)	15 (27.3)
Total	3 (100)	30 (100)	14 (100)	55 (100)

* Number of successful dives, with percent of total successful dives for particular age class in parentheses.

TABLE 3. Comparison among age classes of 102 successful dives as a function of dive height.

Dive height (m)	Age class ^a			
	First-year	Juvenile	Subadult	Adult
1	—	1 (3.3)	2 (14.3)	6 (10.9)
4	2 (66.7)	11 (36.7)	4 (28.6)	17 (30.9)
9	1 (33.3)	12 (40.0)	7 (50.0)	16 (29.0)
15	—	6 (20.0)	1 (7.1)	16 (29.1)
Total	3 (100)	30 (100)	14 (100)	55 (100)

^a Number of successful dives, with percent of total successful dives for particular age class in parentheses.

where n_1 is the refractive index of the first medium (in this case air; $n_1 = 1.00$), θ_1 is the dive angle relative to the water's surface, n_2 is the refractive index of the second medium (seawater; $n_2 = 1.34$, Sverdrup et al. 1942), and θ_2 is the refracted angle relative to the water's surface (Fig. 4). If pelicans sight along their bills, as Schreiber et al. (1975) suggested, then flatter dive angles require pelicans to compensate for prey that are actually located higher above the line of sight; that is, prey are not as deep as they appear (Sustare 1979). The flatter the dive, the greater will be the displacement effect (Fig. 4). The correction necessary for such flat dives may well contribute to the low success rate of inexperienced birds.

Use of steeper dive angles should improve the probability of success in at least two ways. First, a vertical-diving pelican simply reduces its refractive error and improves the accuracy of its line-of-sight aim. Second, the importance of judging prey depth is reduced because prey will be located in the chosen water column, thus increasing the chance of encounter automatically. Dunn (1972) suggested that Sandwich Terns have difficulty judging the position of a deep-swimming prey because of refraction problems, although she did not record the dive angles used by terns. Buckley and Buckley (1974) noted that adult Royal Terns dive more nearly vertical than juveniles. The fact that, in my study, dive angles approached 90° as dive height increased suggests that minimizing refraction is important for pelicans hunting deep-swimming fish.

When prey are at or near the surface, however, pelicans may benefit by switching to relatively flat dive angles. These angles will increase the horizontal volume of water a bird samples. Refractive error is relatively small hunting shallow prey and a bird may do better by increasing its horizontal sampling area.

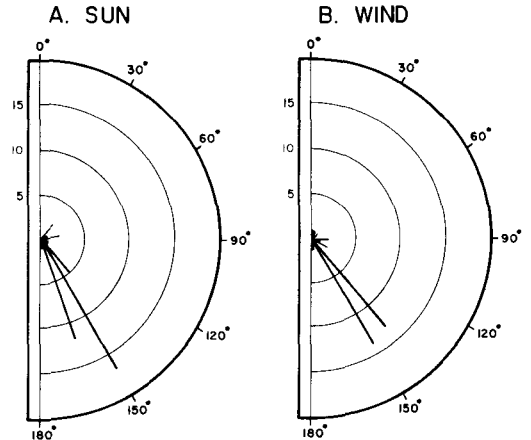


FIGURE 3. (A) Circular histogram indicating head orientation (in degrees) of pelicans, during dives relative to position of sun (sun position = 0°). (B) Histogram showing head orientation (in degrees) of pelicans, during dives relative to wind direction (wind direction from 0°). Numbers adjacent to vertical axes indicate sample size.

Dive height increased as a function of age for Brown Pelicans. Average dive height nearly doubled, increasing by 4.4 m across the four age classes. Dive height has been suggested to be a function of prey depth (Bent 1922, Palmer 1962, Dunn 1972, Schreiber et al. 1975). Increasing dive height can increase the air speed of the bird as it reaches the surface, thus enabling it to dive deeper and, potentially, reach a greater diversity of prey or number of prey. Pelicans have been observed diving from up to 20 m (Murphy 1936). Only 19 (22.1%) of the dives by first-year birds were from heights over 6 m and, of these, only two were greater than 12 m. By contrast, older birds predominately used the greater heights. For example, 71.7% of adults' dives were from heights greater than 6 m and 30.9% were from above 12 m. The gradual development of these "high-dive" skills may be necessary to avoid possible injury during surface impact, to acquire the ability to correct for slight dive errors (e.g., problems in tracking a moving prey item), and to economize on the energetic costs of gaining altitude (especially on windy days). By using greater dive height, an experienced bird may be able to increase its surface sampling area, locate prey more easily, and exploit profitable prey not readily available to birds with lesser skills.

Head orientation can influence the amount of reflected light (glare) and quality of vision aquatic

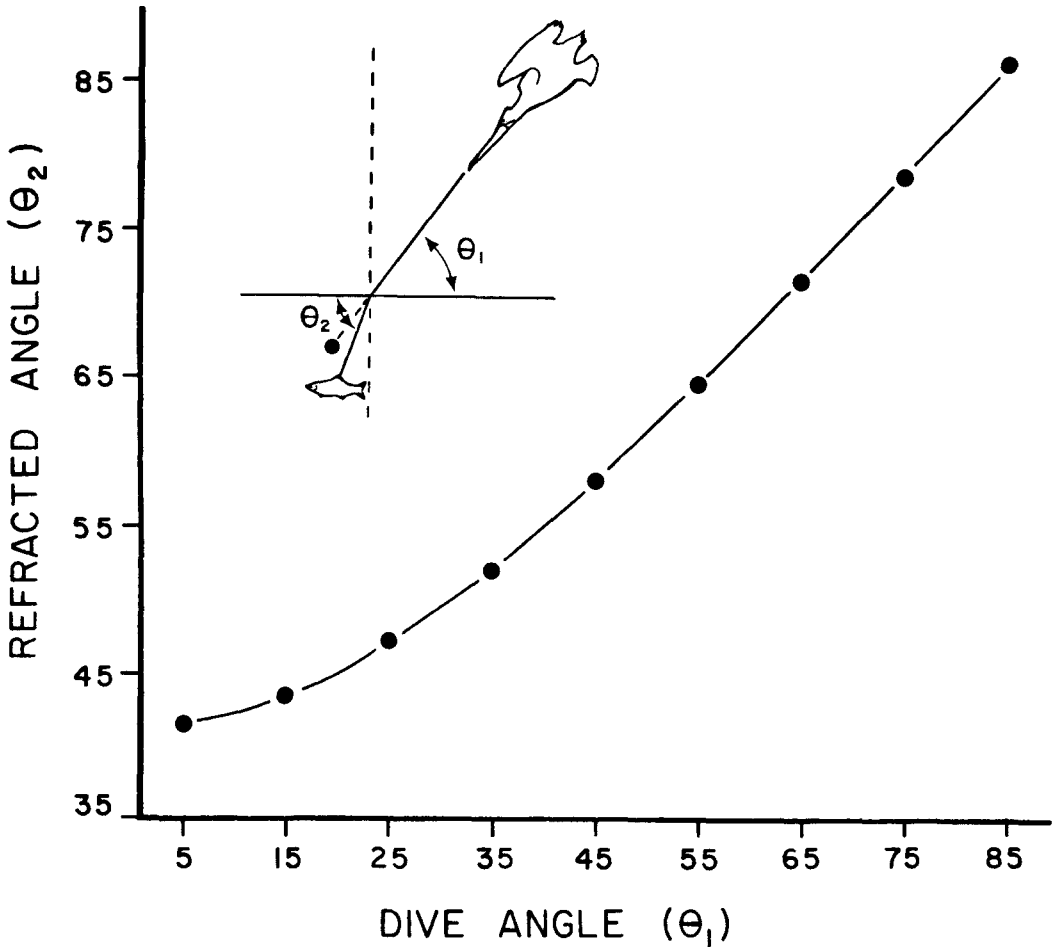


FIGURE 4. Refracted angles (in degrees, relative to water surface) of prey image as would be viewed by a diving pelican. Equation from Huevelen (1982) based on 1.34 refractive index of seawater (at 20°; Sverdrup et al. 1942). Inset shows actual position of prey (solid circle) and position of prey image due to refraction.

birds encounter on sunny days. Buckley and Buckley (1974) suggested that adult Royal Terns hunt early or late in the day in order to reduce glare. Krebs and Partridge (1973) observed that Great Blue Herons (*Ardea herodias*) often used "head tilting" movements when hunting on sunny days and showed that a heron could avoid glare by keeping the back of its head toward the sun.

Brown Pelicans must also contend with highly variable amounts of reflected light from the surface depending on time of day and amount of cloud cover. Potentially, glare could become momentarily disabling on sunny days if a pelican faced the sun directly, especially from a flat dive angle. Lythgoe (1979) suggested that visual im-

age quality is maximized when viewed with the source of light directly behind the observer. The pelicans I observed diving in March 1986 showed a preference for head orientation that minimized reflected light by facing away from the sun (Fig. 3A). Orientation may be less important on cloudy days because reflected light levels are lower.

Wind conditions also may be an important environmental variable for diving pelicans. A tailwind will increase ground speed (Schnell and Hellack 1978), possibly enough that a pelican would gain the momentum necessary to reach deeper prey from a lower dive height. Bent (1922) and Murphy (1936) reported that pelicans usually dive downwind. The head-orientation frequencies presented here likewise reflect a pref-

erence for facing downwind when diving (Fig. 3B). Thus, pelicans may react to sun position and wind direction in parallel. These observations may be an artifact of small sample size but, on the other hand, suggest that Brown Pelicans actively select conditions in which they forage. The effects of weather on foraging success have been demonstrated for several avian species (Grubb 1977, Bovino and Burt 1979, Quinney and Smith 1980). The relationship of sun position, wind direction, and pelican foraging needs further study.

Brown Pelican diving skills improve by the time a bird reaches the juvenile stage, but fine tuning may require at least two more years. Improvement appears as a trend in the use of greater dive heights and steeper dive angles by older birds. This positive association between age and diving skills (which ultimately affect foraging success) may result from involvement of a combination of factors such as light physics, weather, neurological control, and learning. It is likely that first-year birds—lacking experience with changing marine conditions and perhaps not having developed the requisite neurological coordination for using high dives or steep angles—are effectively restricted in choice of foraging times, as well as to prey located relatively near the surface. On the other hand, juveniles and subadults probably are able to exploit deeper prey under a wide variety of conditions, though perhaps not so efficiently as adults.

ACKNOWLEDGMENTS

I thank Stephen Vehrs, Steve Gard, and Bill Leenhouts of the U.S. Fish and Wildlife Service Merritt Island, Florida for their assistance in locating foraging Brown Pelicans. Field assistance was provided by Susan Carl, Larry Govin, and Jim Toothaker. Dan Hough and Frank Sonleitner helped with computer analyses. William Gibbons (Patrick Air Force Base, Florida) provided wind data and Claude Duhon assisted with the evaluation of sun data. I thank Frank Sonleitner, Doug Mock, Gary Schnell, Bruce Coblenz, and an anonymous reviewer for suggestions on various drafts of this manuscript. I am deeply grateful to Gary Schnell for his help and suggestions throughout this project. This paper was submitted as a thesis in partial fulfillment of a Master of Science degree at the University of Oklahoma.

LITERATURE CITED

ALLEN, W. A. 1923. Fishing activities of the California Brown Pelican. *Condor* 25:107-108.
BENT, A. C. 1922. Life histories of North American

petrels and pelicans and their allies. U.S. Natl. Mus. Bull. 121.
BOVINO, R. R., AND E. H. BURTT. 1979. Weather-dependent foraging of Great Blue Herons (*Ardea herodias*). *Auk* 96:628-629.
BRANDT, C. A. 1984. Age and hunting success in the Brown Pelican: influence of skill and patch choice on foraging efficiency. *Oecologia* 62:132-137.
BUCKLEY, F. G., AND P. A. BUCKLEY. 1974. Comparative feeding ecology of wintering adult and juvenile Royal Terns. *Ecology* 55:1053-1063.
BURGER, J. 1980. Age differences in foraging Black-necked Stilts in Texas. *Auk* 97:633-636.
COBLENTZ, B. E. 1986. A possible reason for age-differential success in Brown Pelicans. *J. Field Ornithol.* 57:65-66.
DUNN, E. K. 1972. Effect of age on the fishing ability of Sandwich Terns (*Sterna sandvicensis*). *Ibis* 114:360-366.
FREUND, R. J., AND R. C. LITTELL. 1981. SAS for linear models, a guide to the ANOVA and GLM procedures. SAS Institute Inc., Cary, NC.
GOSS-CUSTARD, J. D., AND S.E.A. LE V. DIT DURELL. 1983. Individual and age differences in the feeding ecology of Oystercatchers (*Haematopus ostralegus*) wintering on the Exe Estuary, Devon. *Ibis* 125:155-171.
GREIG, S. A., J. C. COULSON, AND P. MONAGHAN. 1983. Age-related differences in foraging success in the Herring Gull (*Larus argentatus*). *Anim. Behav.* 31:1237-1243.
GROVES, S. 1978. Age-related differences in Ruddy Turnstone foraging and aggressive behavior. *Auk* 95:95-103.
GRUBB, T. G. 1977. Weather-dependent foraging in Ospreys. *Auk* 94:146-149.
HEUVELEN, A. V. 1982. Physics. A general introduction. Little, Brown and Co., Boston.
KREBS, J. R., AND B. PARTRIDGE. 1973. Significance of head tilting in the Great Blue Heron. *Nature* 242:533-535.
LIST, R. J. 1961. Smithsonian meteorological tables. Smithsonian Institution, Washington, DC.
LYTHGOE, J. N. 1979. The ecology of vision. Oxford Univ. Press, Oxford.
MACLEAN, A. E. 1986. Age-specific foraging ability and the evolution of deferred breeding in three species of gulls. *Wilson Bull.* 98:267-279.
MCCLUNEY, R. 1985. Sun position in Florida. Florida Solar Energy Center publication FSEC-DN-4-83. Cape Canaveral, Florida.
MORRISON, M. L., R. D. SLACK, AND E. SHANLEY. 1978. Age and foraging ability relationships of Olivaceous Cormorants. *Wilson Bull.* 90:414-422.
MURPHY, R. C. 1936. Oceanic birds of South America. Macmillan Co., New York.
ORIAN, G. H. 1969. Age and hunting success in the Brown Pelican (*Pelicanus occidentalis*). *Anim. Behav.* 17:316-319.
PALMER, R. S. 1962. Handbook of North American birds. Yale Univ. Press, New Haven, CT.
QUINNEY, T. E., AND P. C. SMITH. 1980. Comparative foraging behavior and efficiency of adult and juvenile Great Blue Herons. *Can. J. Zool.* 58:1168-1173.

- RECHER, H. F., AND J. A. RECHER. 1969. Comparative foraging efficiency of adult and immature Little Blue Herons (*Florida caerulea*). *Anim. Behav.* 17:320-322.
- ROHLF, F. J. 1982. BIOM statistical programs. State Univ. of New York at Stony Brook, Stony Brook.
- SAS INSTITUTE INC. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute Inc., Cary, NC.
- SCHNELL, G. D., AND J. J. HELLACK. 1978. Flight speeds of Brown Pelicans, Chimney Swifts, and other birds. *Bird-Banding* 49:108-112.
- SCHNELL, G. D., B. L. WOODS, AND B. J. PLOGER. 1983. Brown Pelican foraging success and kleptoparasitism by Laughing Gulls. *Auk* 100:636-644.
- SCHREIBER, R. W., G. E. WOOLFENDEN, AND W. E. CURTSINGER. 1975. Prey capture by the Brown Pelican. *Auk* 92:649-654.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco.
- SUSTARE, B. D. 1979. The physics of light, p. 3-27. In E. H. Burt [ed.], *The behavioral significance of color*. Garland STPM Press, New York.
- SVERDRUP, H. U., M. W. FLEMING, AND R. H. FLEMING. 1942. *The oceans: their physics, chemistry, and general biology*. Prentice-Hall, Englewood Cliffs, NJ.