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FEEDING BEHAVIOR IN LAUGHING GULLS: COMPENSATORY SITE SELECTION BY YOUNG

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ABSTRACT.—Feeding behavior of different age classes of Laughing Gulls (*Larus atricilla*) was studied in different habitats in Texas and Mexico; feeding methods were compared. Adults generally had higher capture success rates and shorter intervals between obtaining food items than young, while subadults were intermediate in both measures. Where food was most readily available (i.e., garbage dumps and fish offal), differences among age classes were negligible. Age differences increased when intervals between obtaining food increased, reflecting the greater difficulty of the feeding task. Proportionately more young fed in those situations where their interfood intervals and success rates most closely approached those of the adults. Young gulls thus appeared to compensate for their generally lower feeding success by feeding at certain sites.

Age differences in foraging behavior and feeding success have been found for several avian species, including Little Blue Herons (*Egretta caerulea*; Recher and Recher 1969), Brown Pelicans (*Pelecanus occidentalis*; Orians 1969), Olivaceous Cormorants (*Phalacrocorax olivaceus*; Morrison et al. 1978), Sandwich Terns (*Sterna sandvicensis*; Dunn 1972), Royal Terns (*S. maxima*; Buckley and Buckley 1974), Glaucous-winged Gulls (*Larus glaucescens*; Barash et al. 1975, Searcy 1978) and Herring Gulls (*L. argentatus*; Verbeek 1977a, b, c, Ingolfsson and Estrella 1978). In general, birds feed more effectively as they gain experience. One measure of feeding effectiveness is the "capture success rate," defined as the number of items obtained per number of capture attempts. Age differences in capture success have been usually attributed to the difficulty of the task (such as plunge-diving which requires a period of learning), or the difficulty in learning to recognize suitable food items, or both. Many aspects of foraging behavior may vary with age, such as the time required to search for prey, pursue the prey once it is found, and capture, handle, and eat the prey. "Search time" may be defined as either the total time a bird searches for food each day or the time required to find individual prey. Search time varies in relation to the ability to find the prey, or the percentage of successful captures, since an unsuccessful attempt lengthens the time required to locate another prey item.

Variations in age differences in foraging within a species under different conditions have not been hitherto studied. We examined the foraging behavior of Laughing Gulls (*Larus atricilla*) under different conditions along the coast of the Gulf of Mexico. We wanted to learn whether age differences in ability varied with the difficulty of the task, and whether habitat use and method of feeding differed with age. We selected Laughing Gulls because they are abundant, feed in a variety of habitats, and use different feeding methods; we chose the Gulf of Mexico region because both adults and young are common there.

We predicted that (1) for difficult tasks young should take longer and/or be successful less often than adults, (2) young should congregate in those areas where the task is easiest, and where their feeding success approaches that of adults, and (3) subadults should be intermediate in ability, approaching adult rates in easier tasks and young rates in more difficult tasks.

STUDY SPECIES AND SITES

The Laughing Gull, a monotypic, hooded gull, breeds locally on the Atlantic coast from New England to Florida and the West Indies, on the Gulf of Mexico to Yucatan, and on rocky islets off the coast of Venezuela and northern Mexico (A.O.U. 1957). The main breeding area is from the Carolinas through the Caribbean. The species winters from the Middle Atlantic states to Peru and Brazil.

We identified three age classes: *adults* (with an all-white tail), *subadults* (resembling adults in body plumage but with a partial narrow subterminal tail band), and *young* (dark-plumaged birds with a broad tail band, see Dwight 1925). In our field work on the Yucatan Peninsula we readily encountered enough young and adult plumaged birds for sampling, but only a small proportion of gulls in subadult plumage.

We studied Laughing Gulls in Galveston Bay and at the Texas City landfill in Texas, near Progresso, 32 km north of Mérida (Yucatán, Mexico), and near Campeche, Champoton, Seybaplaya, and Isla Aguada (Campeche, Mexico). We remained at each study site for at least one day.

METHODS

We examined the foraging behavior of Laughing Gulls along the Gulf of Mexico near Galveston, Texas and in Campeche and Yucatán, Mexico in January 1979. To minimize confounding variables such as season and weather, we limited our study to three weeks, sufficient to study a variety of feeding situations. For four days we observed Laughing Gulls feeding in Galveston Bay and on garbage at the Texas City landfill (where a bulldozer intermittently distributed the garbage over the dump). For the remainder of the study period we studied the gulls on the Mexican Coast. All observations were made on calm, clear, sunny days in order to minimize differences due to weather (see Dunn 1973). We made observations from about 07:00 to 19:00 and did not find age differences in time of feeding. Since we did not mark individuals, our study does not provide information on age differences in the proportion of each day that individuals fed (but see Cooke and Ross 1972, Buckley and Buckley 1974).

We distinguished several methods of feeding (after Ashmole and Ashmole 1967, Ashmole 1971, Simmons 1972): surface-feeding on a garbage dump, aerial snatching, plunge-diving, aerial dipping, and contact-dipping. "Plunge-diving" (where the gulls descend quickly to the water head first, and submerge themselves only partially while capturing fish) was observed at a stream 3 km south of Progresso, at a river mouth 30 km west of Champoton, in the Gulf of Mexico 16 km southwest of Champoton, at Seybaplaya, and behind ferry boats at Galveston, Texas and Isla Aguada (35 km east of Carmen, in Campeche). "Dipping" refers to seabirds dipping only their bills into the water to pick up small food items from the surface. We observed aerial dipping (dipping while flying) at Seybaplaya and Champoton, and contact dipping (dipping while swimming) at Seybaplaya and Progresso Harbor. At Champoton we observed gulls feeding by aerial dipping at a 2-m long dead fish partly exposed in shallow water. At Seybaplaya, a fishing village 55 km south of Campeche City, fishermen butchering sharks tossed offal to waiting Laughing Gulls.

We defined the "interfood interval" as the period between obtaining successive food items. At each feeding location we timed the interfood interval (using a stopwatch) for 20 randomly chosen individuals of each age class. When the gulls were feeding by more than one method, we recorded the interfood interval for 20 randomly chosen individuals of each age class for each foraging method. After timing the interfood interval of one individual we switched to another, alternating age classes. To avoid timing the same individuals repeatedly, we sampled birds in all areas of the flock. We compared the size of food items with the size of the bill and found that at each site, gulls fed on relatively the same size item; age differences within any foraging site thus were not attributable to differences in food particle size. However, since volume and energy values differ among foods, we did not compare foods among study sites or feeding methods.

In addition to interfood intervals, we also recorded capture success rates where possible (success rate = number of items obtained per number of attempted captures). At all study sites, we recorded the number of Laughing Gulls and the age composition every 10 min throughout the observation period, for each method being studied. We made two transects along the Yucatan coast from Progresso to Carmen to count all Laughing Gulls to determine age distribution.

Most analyses were performed using nonparametric contingency tables or correlation procedures (Siegel 1956). Where appropriate, we performed other analyses on interfood intervals (using log-transformed data) and on percentages (using arcsine transformation; Sokal and Rohlf 1969).

RESULTS

In Texas, adults comprised 95% of the foraging Laughing Gulls, whereas along the entire Yucatan coast the ratio of age classes was: 60% adult, 5% subadult, and 35% young. The gulls' choice of feeding habitats ranged from natural (harbors, streams, rivers, ocean) to man-influenced (plunging for fish behind ferries, and over a stream where a culvert had concentrated fish), and to man-made situations (garbage dump, offal). At Seybaplaya, Laughing Gulls fed by a variety of methods within sight of one another: aerial dipping, contact dipping and plunge-diving. Although young comprised only 30% of the gulls present at Seybaplaya, a higher percentage than expected fed by aerial snatching of offal and dipping for invertebrates, and a lower percentage plunge-dived for fish (Table 1). Success rate varied according to feeding method and age (Table 1). Young were as successful as adults when snatching offal in the air, less successful than adults when aerial dipping, and much less successful than adults when

TABLE 1. Effect of age on location of feeding and success rate (df = 2 for χ^2 tests).

	n	Adult	Subadult	Young	χ^2	P
Percent occurrence						
Overall		66	4	30		
Aerial snatching (offal)	200	35	5	60	89.6	0.001
Aerial dipping (invertebrates)	160	55	5	40	7.6	0.02
Plunge-diving (fish)	100	77	3	20	10.8	0.005
Success rate						
Aerial snatching	150	62	60	52	0.4	NS
Aerial dipping	150	96	75	60	6.8	0.05
Plunge-diving	100	83	60	24	12.9	0.005

plunge-diving for fish. Considering occurrence and success rates, young fed mostly where their success rate was closest to that of adults, and avoided feeding where their rate was a third of that of the adults (Table 1). Similarly, while plunge-diving for fish at Progresso Harbor, young were less successful than adults (15% vs. 77%, $\chi^2 = 7.17$, df = 1, $P < 0.01$, $n = 46$).

The interfood interval varied among foraging methods and age classes (Table 2). Intervals were shortest in man-made habitats (dumps, offal), and longest while plunge-diving for fish (except when a school of fish was discovered, Table 2). Comparing all foraging methods, except snatching offal in flight and surface feeding at the dump in the absence of bulldozers, we found statistically significant age differences, with adults obtaining food more quickly than young. Subadults usually had intermediate interfood intervals. Figure 1 shows the relationship between adult interfood intervals and those of young and subadults (data in Table 2). These measures are correlated for adults and subadults (Spearman's $r_s = 0.72$, $n = 9$, $P < 0.05$; Siegel 1956) and for adults and young $r_s = 0.97$, $n = 14$, $P < 0.001$). In general, the young took relatively longer in feeding situations where adults had the longest interfood intervals, and they approached adult intervals where adults had low interfood intervals (Table 2). These results are consistent with prediction 1.

We predicted that young should concentrate their foraging where their interfood intervals were closest to those of adults. Assuming that the adult interfood interval would be related to the difficulty of the task (or the availability of prey), we computed an age efficiency index for the young by dividing the mean interfood interval for the young by the mean interfood interval for adults in each foraging situation (the 14 samples reported in Table 2). A value of 4 indicates that young take four times as long as adults to find food. Plotting the percentage of young in each feeding situation against the age efficiency index (Fig. 2) shows that the proportion of young was negatively correlated with the index (Spearman's rank $r_S = -0.68$, $n = 14$, $P < 0.007$).

We used stepwise multiple regression on arcsine transformation of the percentage of young at each of the 14 feeding situations. Of the independent variables (age efficiency index, interfood interval, capture success rate), the age efficiency index accounted for 54% of the variability in the percentage of young in particular feeding situations ($F = 12.7$, $P < 0.005$), while the youngs' interfood interval accounted for only 25% of the variability in the percentage of young ($F = 4.14$, $P < 0.05$). Thus, merely having low interfood intervals did not cause the young to forage in a particular place. These results indicate that young gulls concentrated their foraging in places where their interfood interval approached the adult interval, further confirming prediction 2.

We likewise examined the feeding of subadult gulls. In five of eight situations where there were enough subadults to sample, their interfood intervals were intermediate to those of adults and young (Table 2). To test whether subadults fared better when feeding was relatively easy, we computed the age efficiency index for subadults versus adults (from Table 2), and examined this in relation to the adult interfood intervals. The two values were positively correlated ($r_s = 0.72$, $n = 8$ cases, $P < 0.05$). Thus it was in the feeding situations where adult interfood intervals were shortest that the subadult intervals were closest to the adult values. In all cases where adult intervals exceeded 4 s, the subadults' intervals were closer to those of the young. While this is consistent with prediction 3, the eight cases represent a small sample, the study having been limited by the paucity of birds in subadult plumage.

DISCUSSION

Age differences in feeding behavior have been found in all gulls and terns examined thus far, although the differences are not consistent

TABLE 2. Interfood intervals (mean ± standard deviation in seconds) for adult, subadult and young Laughing Gulls feeding by a variety of methods. Given are F values from analysis of variance (df = 2, 57,[a] NS = not significant).

Foraging methods	Food	Location	Young	Subadult	Adult	F	P
Surface feeding							
Bulldozer operating	garbage	Texas City	16.0 ± 1.6	8.2 ± 1.1	3.1 ± 1.0	11.9	.001
Bulldozer not operating	garbage	Texas City	9.2 ± 2.2	[f]	8.2 ± 1.2	0	NS
Aerial snatching	offal	Seybaplaya	1.9 ± 1.4	1.8 ± 1.3	1.8 ± 0.9	1.8	NS
Dipping							
Surface	invertebrates	Progresso Harbor	7.0 ± 0.9	5.8 ± 0.8	4.1 ± 0.9	12.8	.001
Surface[b]	invertebrates	Seybaplaya	16.1 ± 3.0	[f]	5.1 ± 2.9	3.1	.01
Surface[b]	invertebrates	Seybaplaya	5.2 ± 0.8	[f]	3.0 ± 0.5	4.70	.001
Surface	fish	Champoton	22.1 ± 2.1	24.1 ± 2.4	12.2 ± 1.2	3.87	.05
Aerial	invertebrates	Seybaplaya	7.2 ± 0.7	3.7 ± 0.8	3.1 ± 0.6	5.48	.01
Plunge-diving							
Behind ferries[c]	fish	Texas	138.1 ± 5.1	[f]	120.1 ± 3.2	12.4	.001
Behind ferries[c]	fish	Isla Aquada	101.2 ± 25.1	[f]	38.1 ± 4.5	22.6	.001
Stream	fish	Progresso	99.1 ± 28.3	55.3 ± 6.5	25.3 ± 6.5	4.53	.001
Ocean[d]	fish	Champoton	89.6 ± 48.0	[f]	19.8 ± 26.1	11.40	.001
Ocean[e]	fish	Champoton	18.2 ± 5.6	16.2 ± 2.3	4.3 ± 0.8	5.83	.001
Ocean[e]	fish	Champoton	6.2 ± 0.5	3.1 ± 0.3	2.3 ± 0.4	13.83	.001

[a] Where only two age classes were considered df = 1, 38.
[b] First sample 100 m from shore, second sample at the mouth of a river that entered the Gulf.
[c] Birds used the ferry as a beater (the motor forced fish to the surface).
[d] Plunge-diving before the discovery of a school of small fish.
[e] Plunge-diving into a school of fish visible from shore.
[f] Quantity of sub-adults not sufficient for statistical comparison.

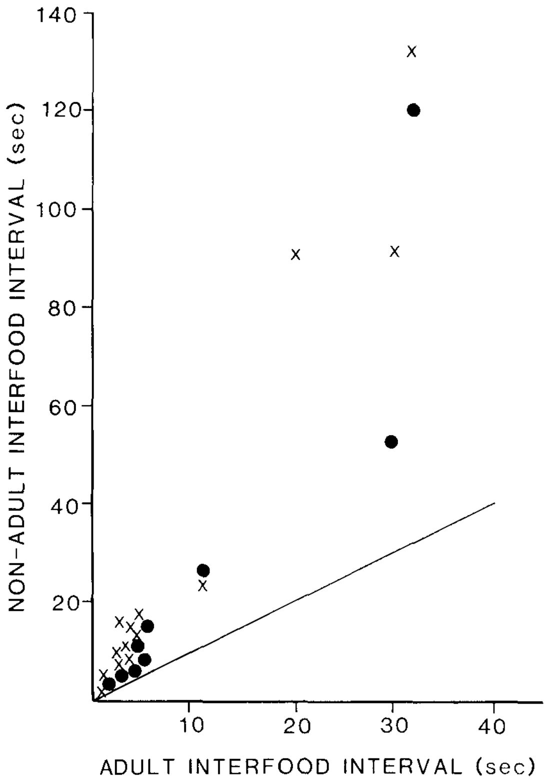

FIGURE 1. Interfood intervals (in seconds) of young (x) and subadult (dots) Laughing Gulls plotted against adult interfood intervals for all foraging situations. The diagonal shows where their rates would be equivalent.

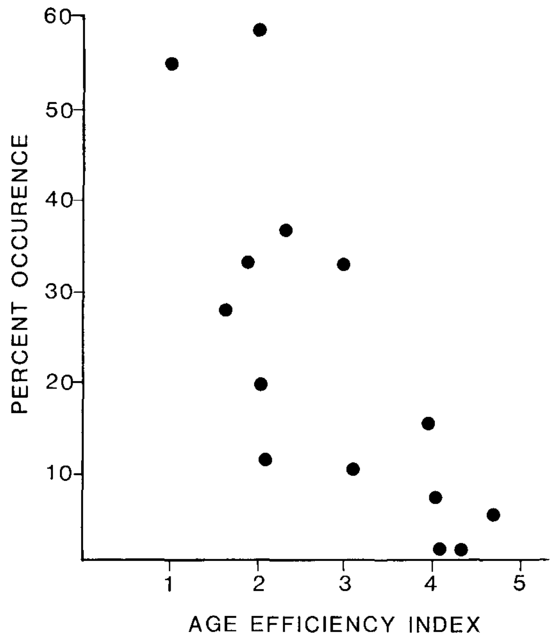

FIGURE 2. Percent of young Laughing Gulls present in each feeding situation in relation to the ratio of mean interfood interval of young divided by mean interfood interval of adults (the age efficiency index).

across species. Verbeek (1977a) found that adult Herring Gulls feeding on starfish were more successful on the first dive, were chased by food pirates less often, and fed on the starfish beds for less time than did immature gulls. Ingolfsson and Estrella (1978) reported that first-year Herring Gulls opened scallops less successfully than did adults. Young had to drop scallops more often, and frequently dropped them on inappropriate (i.e., soft) surfaces. Similarly, Glaucous-winged Gulls differ according to age in ability to open clam shells (Barash et al. 1975) and capture fish (Searcy 1978). The success rates (captures/attempts) for several other species show similar trends, with adults generally being more successful (Table 3). In one of the most extensive studies of the factors affecting foraging success, Buckley and Buckley (1974) found that young and adult Royal Terns had similar capture success rates (captures/unit time), but adults dived twice as often and so obtained more food per unit time than did young.

Differences in success rates may reflect the difficulty of the task and the time required to learn the techniques. It takes time to learn to dive for fish or other invertebrates, to drop clams or scallops on hard surfaces, and to dig for garbage. Evidence that success improves with age was found in young Herring Gulls: their ability to open shells improved from October to April (Ingolfsson and Estrella 1978). Similarly, Burger and Gochfeld (1981) reported that Herring Gull young feeding on a dump improved from September to February in their ability to pirate food from conspecifics and to avoid being victims of other pirates. One must consider, of course, that less successful young may simply starve, leaving the more successful young to be studied.

The distribution and availability of prey are other factors to which birds must respond (Zach and Smith 1981). Age-related differences in habitat use have been reported. Moyle (1966) found that gulls in immature plumage were forced by aggressive adults to feed in suboptimal foraging areas on the edges of a salmon stream in Alaska. Several authors have noted that young gulls often congregate on dumps (Schreiber 1968, Spaans 1971, Cooke and Ross 1972). Presumably food is easier to find or "capture" at a dump than at more traditional feeding habitats or methods (i.e., plunge-diving for fish). Similarly, learning might play less of a role in feeding ability at a dump, compared to other habitats, because food is more abundant, stationary, and not under water or sand. Davis (1975) color-marked Herring Gull family groups, and ascertained that young did not

TABLE 3. Success rates as a function of age for selected species. Shown are sample sizes for the samples (percent success in parentheses).

Species	Feeding success rates[a] Adults	Young	Significance[b] χ^2	P	Method	Source
Brown Pelican	487 (69)	1,482 (49)	59	.001	Plunge-diving	Orians (1969)
Olivaceous Cormorant	773 (18)	1,287 (11)	20	.001	Pursuit-diving	Morrison et al. (1978)
Little Blue Heron	846 (75)	493 (68)	9.9	.01	Walking	Recher and Recher (1969)
Herring Gull	28 (64)	19 (16)	10.8	.001	Diving	Verbeek (1977a)
Glaucous-winged Gull	291 (69)	523 (50)	28.0	.001	Plunge-diving	Searcy (1978)
Laughing Gull						
Fishing—no frenzy[c]	42 (52)	36 (8)	17.1	.001	Plunge-diving	This study
Fishing—frenzy[c]	45 (88)	35 (51)	10.7	.01	Plunge-diving	This study
Swim dipping	40 (94)	40 (80)	4.1	.05	Dipping	This study
Carrion	20 (98)	20 (50)	10.2	.01	Dipping	This study
Offal	120 (65)	50 (52)	4.6	.05	Dipping	This study
Garbage	40 (100)	40 (98)	1.0	.50	Walking	This study
Sandwich Tern	579 (17)	778 (13)	24.0	.001	Plunge-diving	Dunn (1972)
Royal Tern	85 (38)	77 (38)	1.0	.50	Plunge-diving	Buckley and Buckley (1974)

[a] Percent of all attempts that are successful.
[b] Computed by Burger and Gochfeld.
[c] Feeding frenzies are rapid bursts of diving activity localized in a small area.

go to feeding areas with their parents; they fed in a wide variety of locations, and tended to feed farther from their nesting colony than did adults.

Young seabirds can compensate for lower feeding success rates by foraging for a longer part of the day. Such a tendency has been noted for Herring Gull young feeding at dumps and on starfish (Cooke and Ross 1972, Verbeek 1977c, Burger 1981). Young Olivaceous Cormorants foraged longer each day to compensate for their longer feeding intervals (Morrison et al. 1978). Buckley and Buckley (1974) reported that Royal Tern young roosted for less time and at different hours each day than did adults.

Several factors contribute to the age differences in foraging and feeding ability in seabirds including the following: (1) ability to locate feeding areas, and to find and recognize prey, (2) frequency of attempts, (3) ability to capture prey (success rate), (4) appropriate dive heights, and (5) ability to distinguish appropriate surfaces for dropping prey. We believe that a basic problem with our study and others is that another factor, "real search time," was not computed. Investigators have not followed individual birds all day to determine how much time they required to search for feeding habitats (or patches of food). Instead, investigators have observed birds actually feeding, individuals who have already found the feeding habitat. We believe that a "habitat search time," needs to be added to Schoener's (1971) "search time" in order to reflect more accurately the time a gull searches for a given food item. Krebs (1978) discussed foraging models that include the cost of searching for habitats, yet he also noted that there were no data estimating the costs (time, energy) of searching for prey items, particularly when prey are located in patches. We have also found that most studies on feeding in seabirds do not usually include the costs associated with searching for specific prey items once feeding habitats have been located. We therefore suggest that two "search times" need to be measured: the time required to find feeding habitats, and the time required to locate prey. Our measure, the interfood interval, includes the latter.

Another problem with our study is that we selected successful birds, since we did not record an interval until a bird found an item. This biased our data in favor of the most successful birds. It may not bias our relative differences among feeding methods and age classes, but is nevertheless an important variable.

We found that success varied among feeding methods, with adult and young success rates generally increasing together. In this study adults had significantly shorter interfood intervals than young, except at the Texas City garbage dump and while feeding on offal at Seybaplaya (Table 2). The interfood interval of subadults, however, was sometimes closer to that of adults (dipping for invertebrates), sometimes intermediate (plunge-diving in a stream), and sometimes closer to that of young gulls (dipping for carrion). We suggest that the interfood intervals of subadults may reflect the difficulty of the task, where previous experience may be the determining factor.

Interfood intervals varied as a function of foraging method, feeding site, and age. For example, the interfood intervals for adults who were plunge-diving for fish varied from means of 2 to 120 s, and these same values ranged from 6 to 140 s for young (Table 2). Further, the relationship between the interfood intervals of adults and young was not constant from one feeding situation to another. That is, sometimes young required four to five times as long to capture prey (Fig. 2). We found higher percentages of young Laughing Gulls feeding in those habitats and by those methods where their interfood intervals more closely approached the interfood intervals of adults (Fig. 2). Even at one site (Seybaplaya, Table 1), young made up a different percentage of each feeding flock we observed. Although young comprised 30% of the resting flocks, they made up 20% of the flock feeding on fish, 40% of the flock feeding by dipping, and over 50% of the flock feeding on offal. Although birds could see each other within this area, the young elected to feed by methods and on foods where their interfood intervals came closest to that of adults. Our findings demonstrate one behavioral choice available to young to maximize their overall foraging efficiency. Young cannot exercise this option universally because such situations are neither always available nor always predictable, and because the food (e.g., garbage) may not be sufficiently nutritious.

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