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AGE-RELATED DIFFERENCES IN PIRACY OF FRIGATEBIRDS FROM LAUGHING GULLS

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Age differences in foraging success have been reported for a number of avian species. In general, adults have higher attempt rates, have higher capture success, and require less time for foraging than do immatures. Such age-related differences have been noted for Brown Pelicans (*Pelecanus occidentalis*; Orians 1969), Little Blue Herons (*Florida caerulea*; Recher and Recher 1969), Adélie Penguins (*Pygoscelis adeliae*; Ainley and Schlatter 1972), Olivaceous Cormorants (*Phalacrocorax olivaceus*; Morrison et al. 1978), Black-necked Stilts (*Himantopus mexicanus*; Burger 1980) and various gulls and terns (see Burger et al. 1980). Piracy, the stealing of food from other birds, is a particular type of foraging which reduces the difficulties associated with finding food, but requires that birds successfully outmaneuver their victims to obtain food.

Age differences in piracy success have been examined for several species. Verbeek (1977) did not find age differences in piracy rates of Herring Gulls (*Larus argentatus*). Burger et al. (1980) did find significant differences in frequency of attempts, but not in capture success rates for Herring, Ring-billed (*L. delawarensis*), and Laughing (*L. atricilla*) gulls. In this study we examined the piratical behavior of adult and young Magnificent Frigatebirds (*Fregata magnificens*), comparing frequency of attempts, success rates, food handling times, and the circumstances under which piracy was successful.

The pantropical family of frigatebirds is highly specialized for aerial feeding, such adaptations including 40% lower wing-loading than other seabirds of comparable weight (Nelson 1975). Although frigatebirds feed mainly by capturing flying fish and squid from the surface of the ocean, they are well known for pirating food, primarily from boobies, but also from gulls, terns, cormorants, tropicbirds, and shearwaters. Frigatebirds also feed opportunistically on dead fish and on offal from fish (Nelson 1975, Schorger *in* Palmer 1962:380). Nelson (1975) noted that the nutritionally poor seas they inhabit, and their highly specialized feeding techniques, impose on the frigatebirds a prolonged breeding cycle. Frigatebirds, like many seabirds, defer initial breeding for several years (Eisenmann *in* Palmer 1962), which suggests that age groups should differ in feeding (Orians 1969). Except for accounts of differential sex roles and success rates (e.g., Diamond 1972), little is known about circumstances under which frigatebirds engage in piracy. We report here on certain factors influencing success and on age-related differences in piracy.

STUDY AREA AND METHODS

We studied frigatebirds near a fishing dock 2 km SW of the village of Seybaplaya, 55 km S of Campeche, Mexico, on four days in early January 1979. Several boats worked out of the area, returning whenever they were loaded with fish. The fish were cleaned at the dock. Some boats returned each day, so food was available daily, although the timing was not predictable. The fishermen regularly threw offal to the birds. During our visit the dock was frequented by about 100 Laughing Gulls (50–55% in adult winter plumage), 22–25 Sandwich Terns (*Sterna sandvicensis*), 2 Herring Gulls in second winter plumage, and 12–13 adult or juvenile Magnificent Frigatebirds (aged by plumage characters; Eisenmann *in* Palmer 1962).

After observing the behavior of birds while the fishermen threw offal, we obtained a large piece of shark liver, and experimented by throwing various sizes of liver, one piece at a time, to the waiting flock. Small pieces were 25-mm cubes or smaller. Medium pieces were up to 50 × 50 × 80 mm, and large pieces were about 70 × 70 × 80 mm. Using a tape recorder we noted the species and age class of each bird contacting the food, and whether the bird swallowed it immediately, carried, dropped or otherwise lost the food. The tape recording provided a real time base from which handling times could be calculated for each bird in the sequence. We defined the sequence of birds as a chain and determined whether chain length influenced the frequency of piracy. Chain length varied from 1 (if the first bird swallowed the item entirely) to 16. We randomized the sequence of small and medium pieces, and threw a large piece as every tenth item. We provided food at 2 min intervals. In the interval prior to each feeding, gulls circled in front of us, and frigatebirds rose out of the flock to soar in circles about 25 to 50 m overhead. At 10-min intervals we counted the number of gulls in the flock and all frigatebirds in view. Where possible, data were analyzed in 2 × 2 contingency tables.

RESULTS

Frigatebird-gull interactions. When food was not available, gulls and terns rested on the water or on the nearby beach. Frigatebirds were either not in view, or were soaring at altitudes up to 200 m and about 500 m out from the beach. When the the first food item was thrown out, the terns and gulls quickly approached and began feeding. Small pieces of food were swallowed immediately. Some medium-sized and larger pieces were carried away. Other gulls would seize part of these pieces and two birds might tear a piece in half, each swallowing its part. In some cases, the first bird would drop the piece, usually retaining a small bite, or another bird would tear away most of the piece. Large pieces changed beaks up to 15 times, being slightly diminished each time until finally they could be swallowed.

When small pieces of liver were being thrown, there was almost no chasing among the gulls since the pieces were swallowed immediately. Frigatebirds moved in to circle over the feeding gulls, but did not approach closely under such circumstances. Usually two to four males and one to two young drifted overhead about 25 m up. When larger pieces were thrown, chasing among the gulls became common, and frigatebirds entered the flock. Typically they sailed down over the gull holding the food, and from the rear and above either seized the food directly or caused the gull to drop the food.

Although there were usually six adult males, five to six young and occasionally one adult female frigatebird in the area, when large food items were fed, the feeding flocks usually contained three to five males but not more than two juveniles. The young frigatebirds were more likely than the adults to enter the feeding flock at inopportune times. Table 1 shows the frequency with which adult and young frigatebirds entered the

TABLE 1. Comparisons of feeding success measures for adult and young Magnificent Frigatebirds pirating offal from Laughing Gulls.

Measure of success	Adult	Young	Test of significance	
Usual no. individuals in view	6	5–6		
No. bird entries into feeding flock	80	28		
No. piracy attempts[a]	38	22		
No. food items obtained	22 (58%)[c]	6 (27%)[c]	$\chi^2 = 5.3$	$P < .05$[e]
	(27%)[d]	(21%)[d]		$P > .05$[f]
No. food items swallowed immediately[b]	19 (86%)	2 (33%)	$\chi^2 = 9.2$	$P < .01$[g]
No. food items carried away	3 (14%)	4 (67%)		
No. food items lost to pirate	0	3		
Handling times (mean in seconds ± SD)	1.95 ± 1.28	6.00 ± 6.19		$P < .05$[h]

[a] Piracy attempt involves a frigatebird within 1 m of the gull with food, attempting to seize item.
[b] Items swallowed in 2 s or less.
[c] Percent capture success based on number of piracy attempts.
[d] Percent capture success based on number of bird entries into feeding flocks.
[e] 2 × 2 contingency table, chi-square test comparing successful and unsuccessful attempts.
[f] Goodness of fit test based on number of entries of adults and young into feeding flocks.
[g] 2 × 2 contingency table, chi-square test with Yates correction for continuity, comparing number of items swallowed immediately versus items carried away.
[h] Mann-Whitney *U*-test.

feeding flock and their success at obtaining food. Young entered on 11 of 77 occasions when small items were thrown (14%), never obtaining food, while adults entered on only five occasions (6.5%) obtaining food three times.

On 30 occasions when medium-sized and large items were thrown, the chain length exceeded three birds. Adult male frigatebirds were present in the feeding flock on 20 occasions compared with only 7 for young. Adults obtained food 15 times and young obtained food 5 times. Considering the number of individual adults and young entering the flock, the gulls experienced 5.2 times as much exposure to adult frigatebirds as to young. Even when young did not enter the flock they circled within easy flight distance (i.e., less than 100 m) of the gull flock.

Chain length clearly depended on food size. For small pieces, only one instance involved three birds, while for medium pieces the chain was three or more in 29 of 75 cases (39%). The difference is significant ($\chi^2 = 32$, $P < .001$). For large pieces, all 17 chains were three or more, significantly greater than for medium pieces ($\chi^2 = 20.8$, $P < .001$).

Table 2 shows the fate of food items as a function of size and chain length. Gulls swallowed small pieces most of the time, frigatebirds obtaining only 3 of 77 pieces (4%) compared with 25% of medium and 35% of large pieces. Frigatebirds were significantly more likely to obtain medium pieces compared with small pieces ($\chi^2 = 13.9$, $P < .001$) and large pieces compared with small and medium pieces ($\chi^2 = 24.8$, $P < .001$).

Age differences in frigatebird piracy. During 169 feeding trials frigatebirds obtained 28 food items (16.6%). Based on the approximately equal distribution of adult males and young in the area, adults were significantly more successful (goodness of fit, $\chi^2 = 7.1$, $P < .01$) since they obtained 22 items compared to 6 by young. However, considering that adult males entered feeding flocks approximately five times as often as young, the difference in capture success is not significant (goodness of fit, $\chi^2 = 0.43$, $P > .50$), suggesting that once they got into a flock with a medium or large food item, young had an equal likelihood of obtaining the food.

The chance of gulls ultimately losing food to frigatebirds increased with chain length. In chains of four or fewer birds (short chains) frigatebirds got 17 of 152 pieces (11%) while in longer chains they obtained 11 of 21 pieces (52%). Adults caught three food items initially and, although adults entered the flock less frequently than young during short chains, 15 of the 17 items obtained by frigatebirds were taken by adults. In longer chains (thus with larger food items), young and adult frigatebirds obtained food with more similar frequency (four vs. seven).

We compared handling times as a further component of age differences. We defined handling time as the time from seizing an item to losing or swallowing it. Adults usually swallowed food immediately (Table 1) while young did so only 33% of the time. The difference is significant (2 × 2 contingency table with Yates correction for continuity, $\chi^2 = 9.2$, $P < .01$). Handling times averaged 1.9 s for adults and 6.0 s for young (Mann-Whitney $U = 19$, $P < .05$). Longer handling times increased the likelihood of losing food to another bird. Adult frigate-birds did not lose food, while young lost food twice to adults and once to another young (accounting for 50% of the food they obtained from gulls).

In addition to comparing the age-dependent success of the frigatebirds, we examined the age of their gull victims. Although 70% of the birds handling food were adult gulls, 56% of the gulls losing food were young birds. Thus young gulls were victimized proportionately more often than adults (goodness of fit, $\chi^2 = 8.0$, $P < .01$). Adult frigatebirds stole equally from adult and young gulls, while only one of six victims of young frigatebirds was an adult (Fisher Exact Test, $P > .25$).

DISCUSSION

In our study adult male and immature Magnificent Frigatebirds robbed Laughing Gulls and Sandwich Terns that were feeding on fish offal. Diamond (1972) found that female Magnificent Frigatebirds provide most parental care and probably can breed only biennially, while males are apparently free to breed annually. It is no surprise therefore, that Verner (*in* Palmer 1962) reported that at a breeding colony, all piracy was done by females. Nelson (1975) summarized other reports on sex differences in piracy rates, mostly showing that females rob more than do males. If females are more likely than males to occur near a colony, it is reasonable that they should be the main pirates, while males, who are free to wander, will be the predominant pirates away from colonies. Observed sex differences in frequency of piracy thus may reflect whether a particular sex is feeding in a study area rather than basic differences in foraging behavior. The nearest known breeding area to Seybaplaya is at Cayo Arcos, 80 km to the north, where egg-laying occurs in August and September.

Estimates of feeding success vary widely, not only

TABLE 2. Influence of food size and number of Laughing Gulls passing food item (chain length) on piracy success by adult and young Magnificent Frigatebirds.

Size of food item[a]	One to four gulls in chain				Five or more gulls in chain				Mean chain length[b]
	No. of trials	No. food items consumed by[c]			No. of trials	No. food items consumed by[c]			
		Laughing Gulls	Frigatebird			Laughing Gulls	Frigatebird		
			Adult	Young			Adult	Young	
Small	77	74 (96%)	3 (4%)	0	0	—	—	—	1.1
Medium	68	54 (79%)	12 (18%)	2 (3%)	7	2 (29%)	4 (57%)	1 (14%)	2.3
Large	3	3 (100%)	0	0	14	8 (57%)	3 (21%)	3 (21%)	8.0
Total	148	131 (89%)	15 (10%)	2 (1%)	21	10 (47%)	7 (33%)	4 (20%)	

[a] See methods section for sizes of small, medium, and large pieces.
[b] Average number of Laughing Gulls passing food items in each size class.
[c] Refers to the final bird consuming all or part of the food item.

with the method used for estimation, but from place to place. For example, Nelson found success rates for Great Frigatebirds (*F. minor*) pirating from Red-footed Boobies (*Sula sula*) near colonies varied from 12% (Galapagos) and 18% (Aldabra) to 63% (Christmas Island, Pacific Ocean).

In our study we used several methods to compare feeding success. Overall, in 169 feeding experiments adult frigatebirds got food in 13% of the cases and young got food in 3% of cases. However, based on the number of actual attempts when a frigatebird closely approached a gull that had food, adults were successful in 22 of 38 attempts compared to 6 of 22 attempts for young ($\chi^2 = 5.3$, $P < .025$). A third measure of success (see Table 1) is based on the number of birds actually entering a flock. Adults took food on 22 of 80 (27%) bird-entries (including multiple adults in a flock) compared with 6 for 28 entries (21%) for young. Comparing success on this basis reveals no difference in capture success for frigatebirds entering flocks ($\chi^2 = 0.4$, $P > .50$).

Frigatebirds could enhance their chances of success by chasing only birds that are actually carrying food. In the case of terns, which carry food in their bills, this recognition is straightforward. For other species, it is less apparent when they are carrying food. Nelson (1975) suggested that Great Frigatebirds can recognize (perhaps by acoustic cues in the alarm calls) those boobies that have a full esophagus.

Our study revealed a striking difference between adult and young frigatebirds in their tendency to enter flocks. When small food items were thrown and gulls could consume them almost immediately, adult frigatebirds rarely entered the flock. Those that did sought mainly to capture food dropped by the gulls, and the frigatebirds seemed almost as adept as the gulls in seizing food that was being carried by waves onto the rocky shore. By contrast, young frigatebirds frequently entered such flocks. When larger food items were thrown and gulls could not consume the entire item, there was much chasing among the gulls, and the adult frigatebirds quickly swooped into the flock, once with up to five birds present. In such cases, with several frigatebirds and perhaps 40 gulls chasing the bird with food, the young frigatebirds tended to remain just outside the flock. We saw no evidence that adults excluded the young, but suspected that the young were confused by the frenzy of activity and were unable to enter the flock. When young frigatebirds entered the flock and succeeded in singling out a victim, they were as successful as the adults in obtaining the food item. Young frigatebirds had greater success stealing from young than from adult Laughing Gulls, while adults showed no such difference.

Our analysis demonstrates that piracy by frigatebirds depends considerably on the size of the item being captured. Small items swallowed immediately afford no opportunity for frigatebirds to steal food. The larger the piece, the more the piracy among the gulls, and the more chasing. This frenetic activity apparently provides an important cue for the frigatebirds.

Adult frigatebirds obtaining food tended to swallow it immediately, whereas young birds usually carried food for several seconds, frequently losing all or part of it to other frigatebirds.

In conclusion, we found that adult frigatebirds obtained approximately four times as much food per unit time as did young. Adults made more frequent and more appropriate feeding attempts, apparently waiting until there was a good likelihood of obtaining food, and then entering flocks more quickly than did young frigatebirds. Capture success rates by adults and young were not substantially different, although this result would vary, depending on the denominator that one chose (frequency of flock entry, in this study). Adults handled and swallowed food more quickly than young, and young frequently lost all or part of a food item. We believe that this demonstrates substantial age differences between birds in adult and immature plumage. Frigatebirds retain immature plumage for at least three years, during which time considerable maturation and learning must occur.

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COOPERATIVE FEEDING, DEFENSE OF YOUNG, AND FLOCKING IN THE BLACK-FACED GROSBEAK

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The following observations on Black-faced Grosbeaks (*Caryothraustes canadensis poliogaster*) made in a Costa Rican rainforest extend those made by Skutch ten years previously (Skutch 1972). My findings, although limited and dealing with unmarked birds, serve to affirm the likelihood that these birds breed cooperatively and to suggest the possibility of a complex social organization differing from that reported for other cooperative breeders (cf. Brown 1978).

On 3 and 4 July 1978, small, noisy, monospecific flocks of Black-faced Grosbeaks periodically visited a pejibaye (*Bactris gasipaes*) grove at the Organization for Tropical Studies field station, Finca La Selva. At each visit the birds flew together from tree to tree uttering "chu-weet" call notes for several minutes and then left together, flying out of earshot.

On July 4th I saw four adult grosbeaks land on the dried flowering stalk of a bromeliad attached about 6 m above the ground to the trunk of a pejibaye palm. One by one the birds then flew about 1 m down to an open nest in the top of another bromeliad on the same trunk. Each of the four birds fed two young in the nest; each flew away before the next bird descended. Afterwards, the entire flock of grosbeaks left the grove.

On July 5th, J. Dillon also saw four adult grosbeaks feed young at the nest. Later the same day, I saw a flock of six grosbeaks enter the grove but observed only four adults visiting the nest. This time only one perched on the dead flowering stalk before approaching the nest. The other three flew directly to the nest from nearby trees.

Two days later I witnessed group defense of newly fledged young. By 7 July one young had left the nest and was perched less than 1 m above the ground in a low bush. Two or more adults flew near the fledgling, perched next to it and fed it. When I approached within 30 m of the fledgling, the adults flew to a perch about 5 m above me calling loudly (presumably a mobbing call), following which the flock departed.

After many minutes six grosbeaks returned, the bills of several being filled with food. They all perched about 6 m above me, near the nest tree calling loudly ("chu-weet" call). A second fledgling then fluttered down, accidentally colliding with me, at which time the adults' calls increased in intensity. For the next several minutes I captured and released the fluttering fledgling several times. During this period, four and only four of the adults flew to within 3 m of the ground, giving loud "seet-seet" calls incessantly and flying back and forth within 2 to 3 m of me on both sides. These four birds flew close together and in the same direction.

The last time I captured the fledgling it uttered a harsh squeak. The four adults immediately uttered harsh rasping notes not previously heard and flew to within 1 to 2 m of me. One adult, perched 2 m away and about 1.5 m above the ground, spread and vibrated "drooping" wings as for a broken wing display or as if to simulate begging behavior of a young bird. When I released the fledgling the adults resumed their "seet-seet" alarm notes.

When I retreated, the adults approached the fledgling, touching it when I was over 60 m away. During the mobbing I observed one adult at 3 m and noted several pea-sized yellow fruits in its bill, presumably intended for the fledgling. The other two adults participating in the initial mobbing calls had not been evident during the defense of the second fledgling. I interpret these observations of the feeding and defense of young by at least four adult-plumaged birds together with the observations by Skutch (1972) as sufficient evidence for the existence in this species of cooperative breeding as defined by Lack (1968; see also the review by Brown 1978).

Three specific points noted during the observations suggest that monospecific flocks of this species may be complex, composed of breeders, helpers, and a variable number of "hangers-on": 1) the size of the groups coming near the nest was variable, including eight or more individuals; 2) despite the presence of six to eight birds near the nest, I never saw more than four different birds feed the young during a single visit; and 3) only four adults of the six present defended the young. The defense of young by a subset of the birds was particularly important in suggesting that only they were actually involved with the breeding, as either breeders or helpers. Even though the birds were not marked, I was able to determine with certainty that during the defense and the occasions when adults fed the young, four individuals were involved. In each case all four birds were visible simultaneously and did not fly out of my sight during the episodes described. I cannot say whether these four birds were the same on each occasion, but I think the possibility is likely. Skutch (1972) described a pattern similar to that noted in points 1) and 2).

Two other observations are relevant to the pattern suggested above. The groups of grosbeaks visiting the nest to feed the young did so periodically with relatively long absences between visits. Flocks of grosbeaks that I saw elsewhere at La Selva during the same