BROWN PELICAN FORAGING SUCCESS AND KLEPTOPARASITISM BY LAUGHING GULLS

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ABSTRACT.—Previous studies have shown age-related differences in feeding success for a number of bird species, particularly those found in marine environments. We compared the foraging success of adult and immature Brown Pelicans (*Pelecanus occidentalis*) feeding along the Playa Miramar northwest of Manzanillo, Colima, Mexico. On many of the feeding dives, Laughing Gulls (*Larus atricilla*) were attracted to pelicans and often behaved aggressively in attempts to obtain food from them. Adult Brown Pelicans were significantly more successful than immatures. Laughing Gulls were attracted to successful pelicans regardless of the age of the pelican. The proportion of unsuccessful immature pelicans not attracting gulls was higher than that of unsuccessful adult pelicans. Particularly inept immature pelicans are probably easily identified by gulls and ignored completely. Although we found no differences in the frequency of pelican-gull physical contact (which we used as a measure of gull aggressiveness) between immature and adult pelicans, such behavior was directed almost exclusively toward successful pelicans. Gull aggression was also more intense when pelicans were attacked by groups of gulls. *Received 26 May 1982, accepted 21 March 1983.*

A GROWING number of studies document that, when birds such as Brown Pelicans (*Pelecanus occidentalis*) use relatively complex hunting techniques, a fine-tuning of abilities develops with age (e.g. Morrison et al. 1978, Searcy 1978, Quinney and Smith 1980). In some species, because of behavioral differences between successful and unsuccessful foragers and age-related plumage variation, it is relatively easy to quantify differential feeding success between age classes in the field. For example, such plumage variation enabled Orians (1969) to gather data documenting differences in hunting success between diving adult and immature Brown Pelicans.

Age-related differences in foraging success could influence interspecific feeding interactions. For instance, birds pirating food from members of another species might preferentially seek out birds of a particular age as potential victims if they were better foragers or more likely to surrender food when attacked. Of course, age indicators and the associated likelihood of host success may not be cues used by a potential kleptoparasite. Rather, a potential pirate may simply recognize some other characteristic typical of a successful host and attack before the latter has a chance to consume a particular food item. Although an extensive body of literature exists concerning kleptoparasitism in birds (Brockmann and Barnard 1979), investigators have not examined the interactive effects of age and success of the host on the probability of attempted theft by another species, nor is there documentation available relating the extent of aggressiveness of the parasitic species to host success or age.

Brown Pelicans and Laughing Gulls (*Larus atricilla*) are often found in close association, and Bent (1921) and Baldwin (1946) recorded instances of these gulls kleptoparasitizing pelicans. Although they provide qualitative descriptions of such gull-pelican interactions, the association has not been quantitatively assessed. Both Brown Pelicans and Laughing Gulls are common and easily observed in the vicinity of Manzanillo, Colima, Mexico during the winter months. Thus, while conducting fieldwork in this area in January 1982, we had the opportunity to record feeding interactions of these two species. We quantified feeding success in adult and immature pelicans and recorded numerous instances of attempted theft from Brown Pelicans by Laughing Gulls. We hypothesized that: (1) gulls should be attracted more often to successful pelicans; (2) if adult Brown Pelicans are more successful than immatures, Laughing Gulls should be attracted preferentially to adults; and (3) aggressive behavior directed by gulls toward pelicans should

increase when successful adult pelicans are targets for theft.

Methods

Observations were made on 9 and 10 January 1982 along the Playa Miramar on Bahia Santiago, located approximately 10 km northwest of Manzanillo in the State of Colima, Mexico. The flat, white-sand beach is regularly used by vacationers. In addition, as many as 140 Brown Pelicans were found actively feeding along the beach for extended periods during the day, and at least 500 gulls were present in the general vicinity. The majority of the gulls were Laughing Gulls, although a few Bonaparte's Gulls (*L. philadelphia*) and an occasional Heermann's Gull (*L. heermanni*) were observed. Virtually all of our observations involved Laughing Gulls.

During observation periods on each of the days, skies were clear and it was relatively calm, with waves averaging approximately 1 m in height. Six pairs of observers were positioned at least 100 m apart along approximately 1.2 km of beach. Pelicans were feeding in the surf, usually less than 50 m from the shoreline; thus, it was relatively easy to record feeding success and pelican-gull interactions. Individuals observed birds through binoculars or with the unaided eye. We chronicled: (1) time of day; (2) whether the diving pelican was in adult or immature plumage; (3) whether the pelican was successful or unsuccessful in its attempt to capture prey; (4) the number of gulls attracted to a surfacing pelican; and (5) whether or not gulls, if attracted, actually came into physical contact with the pelican. Operationally, any gull within about a meter of a pelican (sometime during the period between its surfacing and its swallowing or draining water from its bill) was counted as having been attracted to the pelican. Body contact was our measure of gull aggression; gulls initiated contact and often pecked the victim.

Our criteria for pelican feeding success were those developed by Orians (1969) and Schreiber et al. (1975). They found that unsuccessful pelicans simply allow water to drain from the gular pouch upon completion of a feeding dive. Successful individuals hold the bill close to the breast while water drains out and subsequently swallow with an obvious head-tossing motion. Because plumages of adult and immature Brown Pelicans are distinct, the age of the focal bird was easily determined. In January, the immature plumage characterizes birds hatched during the previous breeding season.

All statistical tests were conducted on frequency data. Some analyses involved two-by-two tests of independence using the *G*-statistic (Sokal and Rohlf 1981), where the resulting statistic is compared to the critical Chi-square value with one degree of freedom. We also analyzed three-way contingency tables using log-linear models (Knoke and Burke 1980, Sokal and Rohlf 1981), which, for attribute data, correspond to linear models in analysis of variance and multiple regression for continuous variables. The significance of a term in the overall log-linear model is tested by calculating the difference between the *G*-values for models with and without the term. These calculations were completed using BMDP program number P3F (Dixon and Brown 1979).

As indicated by Brown (1976) and Dixon and Brown (1979), testing for any particular effect (e.g. the interaction of factors A and B) depends on the other effects included in the particular log-linear model. Thus, several appropriate ways exist for evaluating the strength of a given effect. They suggested using two tests—those involving marginal and partial associations—to determine the significance of an effect. These two estimates of importance and their associated *G*-values provide similar, although not necessarily identical, statistical findings. Dixon and Brown (1979) imply that, if for a given effect one test results in a statistically significant value while the other does not, the effect is probably of only minor importance. When tests for complete independence or the highest-order interaction (in our case the three-way interaction) are conducted, marginal and partial associations do give identical numerical results. Additional details concerning the use and theory of log-linear models in the analysis of multiway contingency tables are given in Brown (1976), Dixon and Brown (1979), Knoke and Burke (1980), and Sokal and Rohlf (1981).

Results

We recorded information on a total of 2,449 pelican dives. Adults were more successful than immature birds at capturing prey; overall success differed by 9.2% between the two groups (Table 1). Tabulated significance values indicate that, during four of the six subperiods, this trend was statistically significant, as it was when we considered the summed frequencies. The two subperiods not exhibiting statistically significant differences between ages were those for which sample sizes were the smallest.

The pelicans were feeding on relatively small fish (most of which were less than 15 cm in length), probably of several different species. Fish of this size were abundant in the shallow waters along the beach during the period of our visit.

On both days pelicans began to feed actively soon after sunrise. By 1000, a number of the pelicans were resting on the water, often in rafts of birds, and after 1030 very few individuals were seen diving. Relatively few pelicans fed in the afternoon, compared to early morn-

TABLE 1. Percentage of successful dives by adult and immature Brown Pelicans.

Date and time	Percentage successful (successful/total)		G-value[a]
	Adults	Immatures	
9 January 1982			
0900–1000	88.5 (207/234)	81.9 (281/343)	4.69*
1000–1100	72.9 (43/59)	78.0 (64/82)	0.50
1430–1530	82.2 (37/45)	75.9 (101/133)	0.79
10 January 1982			
0830–0900	79.7 (110/138)	63.3 (167/264)	11.95***
0900–1000	83.1 (157/189)	72.7 (240/330)	7.41**
1000–1100	85.4 (205/240)	76.8 (301/392)	7.19**
Total	83.9 (759/905)	74.7 (1,154/1,544)	28.74***

[a] Two-by-two G-test of independence, with factors being age (adult and immature) versus success (successful and unsuccessful). * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

ing. During the afternoon, pelicans in the vicinity of the beach would take flight, feed for a while, and then land again in the area or fly toward a large raft of birds on the water off a point of land about 2–3 km away. The very active periods of feeding in the morning were associated with times just before the high tide (based on data from National Oceanographic and Atmospheric Administration, U.S. Dept. Commerce). Because data are available for only two consecutive days, however, we do not have information from days when the high tide did not occur during the morning daylight hours.

Because, when making observations, we recorded pelicans irrespective of their age, the proportions of adults and immatures obtained (Table 1) are good estimates of the relative numbers of the two age groups feeding at any particular time. On the morning of 9 January (0900–1100), 59.2% of the observations were of immature Brown Pelicans. The comparable value for the morning (0830–1100) of the next day was 63.5%. We found that 74.7% of the pelicans feeding in the afternoon (1430–1530) on 9 January were immature birds.

For each pelican dive, we tabulated the age and success of the pelican and the number of gulls that were attracted to the pelican (Table 2). Clearly, unsuccessful pelicans did not often attract gulls; in contrast, over 70% of successful pelicans drew in one or more gulls. The results of a three-way evaluation of frequencies (Table 2) for pelican age, pelican success, and number of gulls attracted are presented in Table 3 (Evaluation A). The three factors are interrelated as indicated by the overall test of independence. We did not find a significant three-way interaction, but two-way associations are evident. The strongest two-way dependency was found for pelican success and number of gulls present—gulls associate themselves with successful pelicans. Age and success are also related in that, as indicated earlier, adults are more successful hunters than immatures are. Different results in terms of statistical significance were obtained depending on whether partial

TABLE 2. Observations of diving Brown Pelicans classified as to age, success at capturing prey, and the number of gulls attracted.

Number of gulls attracted	Adult pelicans[a]		Immature pelicans[a]	
	Successful	Unsuccessful	Successful	Unsuccessful
0	185 (24.4)	79 (54.1)	281 (24.4)	258 (66.2)
1	189 (24.9)	27 (18.5)	327 (28.3)	57 (14.7)
2	195 (25.7)	24 (16.4)	269 (23.3)	47 (12.1)
3	97 (12.8)	10 (6.8)	165 (14.3)	16 (4.1)
>3	93 (12.3)	6 (4.1)	112 (9.7)	12 (3.1)
Total	759	146	1,154	390

[a] Percentages within a particular pelican age and success category are given in parentheses.

TABLE 3. Summary of statistical evaluations of three factors—pelican age, pelican success, and number of gulls attracted—based on log-linear models.

Hypothesis tested	df	G-value[a]	
		Partial association	Marginal association
Evaluation A (gull categories 0 to >3)			
Age × success independence	1	21.18***	28.75***
Age × number of gulls independence	4	7.27	14.84**
Success × number of gulls independence	4	269.18***	276.75***
Age × success × number of gulls interaction	4	6.18	
Age × success × number of gulls independence	13	318.94***	
Evaluation B (gull categories 1 to >3)			
Age × success independence	1	2.45	2.69
Age × number of gulls independence	3	5.99	6.23
Success × number of gulls independence	3	8.95*	9.19*
Age × success × number of gulls interaction	3	0.96	
Age × success × number of gulls independence	10	18.83*	

[a] Both partial and marginal associations are used to test independence and interactions. Results of tests for marginal and partial associations are equal when evaluating complete independence or the highest-order interaction. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

or marginal associations for pelican age and number of gulls were analyzed (Table 3), suggesting only a relatively weak interaction, caused primarily by differences between unsuccessful immature and adult pelicans (see Table 2).

Because unsuccessful pelicans seldom attracted gulls, we further analyzed a subset of our data to investigate interdependencies, if any, when at least one gull was attracted to a pelican. Figure 1 depicts percentages of total observations within the four pelican age-success groups where from one to more than three gulls were attracted (i.e. observations in the zero-gull category of Table 2 were ignored and percentages recalculated for the other four categories). The overall three-way test of age, success, and number of gulls indicated a significant interdependence (Table 3, Evaluation B). No three-way interaction effect was found, suggesting that the degree of association between any pair of factors is independent of the particular grouping within the third factor. Age and success were found to be independent, implying that (after deleting data on pelicans that did not attract gulls) adults and immatures did not differ in their success at capturing prey. Also, the two-way test of age and number of gulls was nonsignificant, indicating that among pelicans attracting gulls there is no difference in the number of gulls drawn to adult and immature pelicans. The test of independence between pelican success and number of gulls attracted was significant, however; successful pelicans of both age groups tend to attract multiple gulls (i.e. three or more than three) more often than do unsuccessful birds (Fig. 1).

Sometimes the gulls attracted to pelicans made aggressive physical contact with them while attempting to pirate some of the captured prey. During the afternoon of 9 January and on 10 January, we recorded whether or not contact was made during a theft attempt. Table 4 summarizes observations of dives categorized as to success, age, number of gulls, and contact. Contact almost never occurred between gulls and unsuccessful pelicans, irrespective of the number of gulls attracted. The finding is further substantiated by a two-by-two test of independence involving the following four combinations: successful and contact, 266 observations; unsuccessful and contact, 9; successful and no contact, 768; unsuccessful and no contact, 145. The G-value of 37.88 ($P < 0.001$) indicates that the two factors—success and contact—are highly interdependent.

Records of successful pelicans were further analyzed in a three-way test of independence. Factors considered were pelican age, frequency of pelican-gull contact, and the number of gulls attracted. The overall evaluation indicated the presence of interdependencies among the three variables (bottom line of Table 5). Also, the three-way interaction factor was significant, suggesting that the relationship of any two factors is in part dependent on the category of the

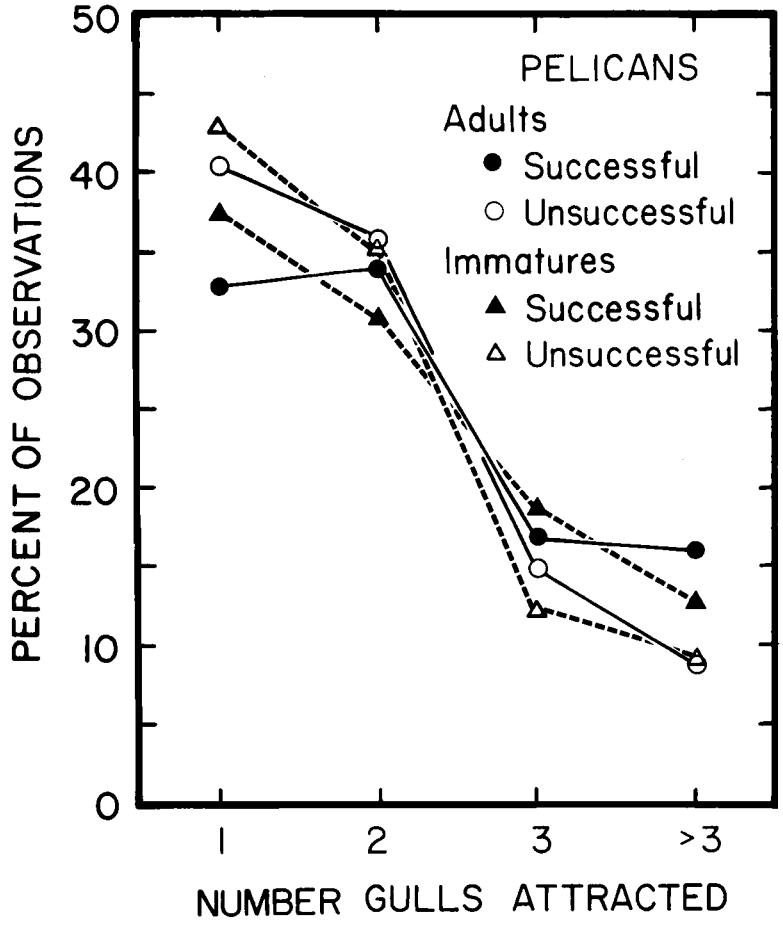

Fig. 1. Percentages of diving Brown Pelicans that attracted one to more than three gulls. Percentages calculated within each of the four age-success categories and based on a subset of data presented in Table 2 (i.e. observations of pelicans that did not attract gulls were deleted).

third factor. No association was found between age and contact, showing that there were no differences in the frequency of gull-pelican contacts between successful adult and immature gulls. Again, the two-way test of age and number of gulls attracted gave a nonsignificant result, implying that the number of gulls attracted was not different for the two age groups. A strong interdependence was found for contact and number of gulls attracted, however; the proportions of observations involving gull-pelican contact were much higher when more gulls were involved.

DISCUSSION

Many studies have shown age-related differences in feeding success in birds, with older birds typically being more efficient (recent reports include Ulfstrand 1979, Burger 1980, and Quinney and Smith 1980). Among the Pelecaniformes, Olivaceous Cormorant adults (*Phalacrocorax olivaceus*; Morrison et al. 1978) and Brown Pelican adults (Orians 1969) are known to be more successful foragers. Our results, with respect to enhanced foraging success of adult over immature Brown Pelicans, correspond with Orians' (1969) findings. Brown Pelicans plunge-dive for fish, a technique that requires a particular degree of skill (Schreiber et al. 1975). Both diving skills and facile use of the mandibular apparatus may increase hunting proficiency with increasing age and experience. Mortality during the first year of life is estimated to be from 70% to 75% for Brown Pelicans (Schreiber 1976), much of which may be due to the in-

TABLE 4. Number of observations of gulls attracted to Brown Pelicans of different ages and success, with indication of whether physical contact occurred between gulls and pelicans.

	Number of gulls attracted and contact							
	1		2		3		>3	
Pelicans	Yes	No	Yes	No	Yes	No	Yes	No
Successful								
Adults	23	100	21	113	28	44	37	37
Immatures	36	184	50	143	33	97	38	50
Unsuccessful								
Adults	3	17	2	16	0	7	0	2
Immatures	1	42	1	39	1	13	1	9

ability of many younger birds to master plunge-diving skills (R. W. Schreiber unpubl. obs.).

Immature Brown Pelicans might be expected to compensate for their relative foraging inefficiency by hunting for longer periods of time than adults. Adult Royal Terns (*Sterna maxima*; Buckley and Buckley 1974), Olivaceous Cormorants (Morrison et al. 1978), and Black-necked Stilts (*Himantopus mexicanus*; Burger 1980) spend less time foraging than do immatures. Although we have limited data concerning this point, there is some evidence that immature Brown Pelicans feed for longer periods of time. The proportion of hunting pelicans that were immatures was perceptibly higher in the afternoon than in the morning. During the afternoon hours, many of the pelicans were loafing in the large raft of birds located some distance from the feeding area. Presumably, the proportion of nonfeeding adults relative to immatures in the raft was higher than among the feeding birds in the afternoon.

Brockmann and Barnard (1979) proposed that kleptoparasitism may evolve wherever individuals of different species associate regularly in large numbers near feeding areas, as is the case for Brown Pelicans and Laughing Gulls over a wide geographic range. Although most detailed studies of kleptoparasitism have been done in or near breeding colonies (Brockmann and Barnard 1979), conditions favoring parasitism also exist where potential hosts and kleptoparasites congregate regularly in large winter foraging flocks (Ingolfsson 1969, Källander 1977, Burger 1981). Even with large numbers of potential hosts, kleptoparasitism would be a poor food-capturing technique if parasites could not distinguish between potential hosts carrying food and those without prey. When food items can be easily seen, pirates may concentrate their attacks on hosts carrying prey of particular types or sizes (e.g. Dunn 1973, Fuchs 1977). During our investigation, pelicans were feeding on rather small-sized prey, and, thus, when pelicans surfaced, the gulls probably could not see the fish that had been captured. As predicted in our initial hypothesis, however, Laughing Gulls preferentially attacked Brown Pelicans that caught prey, while often ignoring those pelicans surfacing without fish.

TABLE 5. Summary of statistical evaluations for three factors—pelican age, gull-pelican contact, and number of gulls attracted—computed using data for successful Brown Pelicans and based on log-linear models.

		G-value[a]	
Hypothesis tested	df	Partial association	Marginal association
Age × contact independence	1	0.17	0.60
Age × number of gulls independence	3	5.49	5.92
Contact × number of gulls independence	3	50.40***	50.83***
Age × contact × number of gulls interaction	3	9.84*	
Age × contact × number of gulls independence	10	66.76***	

[a] Both partial and marginal associations are used to test independence and interactions. Results of tests for marginal and partial associations are equal when evaluating complete independence or the highest-order interaction. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Clearly, gulls were cuing on something other than our indicator of hunting success (i.e. head tossing), because gulls typically attacked considerably before this behavior took place. Of course, this is not surprising, as there would be no advantage to attacking a pelican that had just swallowed its prey.

A second prediction was that, if adult pelicans are more successful than younger birds, gulls should be attracted preferentially to adult birds. Relatively little if any support of this hypothesis was found. If only successful pelicans are considered, there is no difference between adults and immatures in the relative numbers of gulls attracted (see Table 2). If the category for no gulls being present is deleted, no difference in number of gulls attracted is evident (Evaluation B, Table 3; Fig. 1), whether it be for successful or unsuccessful pelicans. The only differences in pelican-gull interactions relating to pelican age involve unsuccessful pelicans. The percentage of unsuccessful immatures not attracting gulls is higher than that for adult pelicans (Table 2), and there are relatively more unsuccessful young than adult pelicans (Table 1). Diving pelicans that are particularly uncoordinated or inept are probably easily identified by gulls and may be ignored by them. We observed a number of young pelicans that surfaced after a dive without their pouches inflated, thus clearly signaling that these birds had not caught fish. Except for this subgroup of unsuccessful pelicans, it seems likely that Laughing Gulls do not discriminate between immature and adult pelicans. Rather, they concentrate attentions on successful pelicans irrespective of their ages.

The greater attention of gulls to successful pelicans was also reflected by the number of gulls attracted, with many gulls being found more frequently around successful than unsuccessful pelicans (Fig. 1). Hatch (1970) suggested that Laughing Gulls kleptoparasitizing terns responded to other gulls chasing terns rather than to the victim itself or the food item; the initiator of a chase, however, probably responded to host success. A benefit to joining a group of prospective pirates is that the likelihood of a potential victim losing its prey increases as the number of attackers rises (e.g. Hatch 1970, Hulsman 1976, Taylor 1979). The pelicans we studied were taking small-sized fish and captured a number of fish in a single dive. The pelicans might well drop several fish at a time when closely attended by a group of gulls. Thus, all of the gulls harassing a pelican may have a relatively good chance of obtaining food. It is also possible that a shortage of potential victims could indirectly result in groups of gulls attacking single pelicans (e.g. Hatch 1975). Such could have been the case along the Playa Miramar given that gulls considerably outnumbered pelicans. The aforementioned advantages of groups probably still apply, however, even if groups initially form due to a shortage of available hosts.

Our third hypothesis indicated that aggressive behavior of gulls toward pelicans should be more prominent when successful adult pelicans are involved. We recorded the frequency of physical contact between gulls and pelicans as a measure of aggressiveness. While no differences were found in the frequency of contact for the two age classes, physical contact by gulls was, with only a few exceptions, restricted to successful pelicans (Table 4). Furthermore, contact was more frequent when groups of gulls were pursuing a pelican.

Bent (1921) and Baldwin (1946) reported that Laughing Gulls sometimes land on the head of a Brown Pelican and take food from its beak. Also, Baldwin (1946) noted that pelicans "never show anything but stoic calm during this procedure." Many of the pelicans we watched, however, reacted to the close proximity of gulls by taking flight as soon as water drained from their pouches. At other times they behaved aggressively toward the gulls, and, in two instances, we saw a pelican seize a gull with its bill and toss the bird aside. Clearly, pelicans were often irritated by the gull activity; furthermore, gulls attempting to kleptoparasitize pelicans risked the chance of physical retaliation by the potential host. Thus, it is not surprising that gulls were more assertive when more than one was provoking a pelican. Under this circumstance, there is probably a decreased chance that a particular gull would be the victim of retribution.

Harassment of a possible host, involving physical contact, is likely to increase the chance that it will release captured food items. In the only investigation of this general topic, however, Andersson (1976) found no increase in the probability of Northern Gannets (*Sula bassanus*) regurgitating when Great Skuas (*Catha-*

racta skua) touched their potential victims. Although we did not quantify the frequency of successful kleptoparasitism relative to whether or not physical contact occurred, our subjective assessment is that such aggressive behavior produced a beneficial result for the gulls, especially when the gull is part of a group. This may have been particularly likely given the small size of prey taken by the pelicans in our study, because even a slight opening of a pelican's bill could result in the loss of captured fish.

Detailed quantitative information was not recorded as to the success of gulls in obtaining food from pelicans, in part because of the small size of fish being captured. We did, however, make three observations of fish being taken from a pelican by a gull. Also, during our study S. P. Carroll and K. L. Cramer (unpubl. ms) recorded 20 instances of gulls obtaining fish when in close association with surfacing pelicans. Certainly, these instances and the many other gull-pelican interactions we observed were not chance associations between the two species, but rather encounters initiated by the gulls. Overall, it appeared to us as if kleptoparasitism was a highly beneficial activity from the standpoint of the gulls. It will be necessary, however, to quantify gull success and other factors in order to demonstrate this point convincingly. It should be possible (albeit somewhat difficult) to evaluate food losses by pelicans as a result of interactions with gulls quantitatively. This information, coupled with estimates of energetic demands of gulls and pelicans engaged in pursuit and evasive actions, respectively, would enable future workers to couch their investigations in terms of common cost and benefit units.

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