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SELECTION OF PREY AND SUCCESS OF SILVER GULLS ROBBING CRESTED TERNS

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ABSTRACT.—Silver Gulls (*Larus novaehollandiae*) stole fish from Crested Terns (*Sterna bergii*) at One Tree Island, Great Barrier Reef, Australia. They attempted to steal larger fish of several kinds more often than smaller ones up to a point, but did not try to steal the largest fish most frequently. Silver Gulls preferred disc-like fish 8–10 cm long and cone-like fish 14–16 cm long. The likelihood that gulls would try to steal a fish was influenced by such factors as its length, weight, shape, and availability, of which weight appeared to be particularly important. Robbing success differed significantly with length in only three of the 11 types of prey available. Gulls robbed in various ways, the success of which depended on a tern's maneuverability, method of evasion, and speed of reaction to pirates.

Many birds steal food from other birds (see Brockman and Barnard 1979 for a recent review). Many variables appear to affect the frequency and success of such behavior: (1) the number of potential victims and pirates in a colony (Dunn 1973, Veen 1977); (2) the relative size of the pirate and its victim (Corkhill 1973, Hulsman 1976); (3) interference from conspecifics (Hulsman 1977c); (4) the number of pirates chasing a victim (Hatch 1970, 1975; Hulsman 1976) and the duration of the chase (Furness 1978); (5) the victim's reactions to a pirate (Furness 1978); (6) the method used by a robber to steal a food item (Hulsman 1976); (7) the size of the food item (Hopkins and Wiley 1972, Dunn 1973, Hulsman 1976, Veen 1977); and (8) weather conditions (Hatch 1975, Veen 1977). However, the effect of prey type on the frequency and success of such piracy has not been examined in situations where a robber can choose between several types of food. In addition, the stimulus (or stimuli) to which a robber responds has not been determined, although the length (Hulsman 1976) and the weight (Dunn 1973) of a prey item seem to be important.

Silver Gulls (*Larus novaehollandiae*) in colonies of Crested Terns (*Sterna bergii*) commonly steal food from the latter (Hulsman 1976, 1977c). They are particularly good subjects for studying prey selection because the food items that they steal can be readily measured and identified. Furthermore, Crested Terns eat a variety of fish (Hulsman 1977c) allowing one to study how prey size and type influence robbing behavior. In this paper, I examine whether gulls select prey on the basis of their length, weight, type, shape, or relative abundance.

STUDY AREA

My study area was One Tree Island (23°31′S, 152°06′E) in the Capricorn Group at the southern end of the Great Barrier Reef, Australia. The island is small (4 ha) and largely covered by a low shrub, *Melanthera biflora.*

Crested Terns often nested on a succulent herb, *Sesuvium portulacastrum,* which surrounds a shallow tidal pond on the island (Hulsman 1977b, c). During 1974–1975, for example, 432 pairs of terns nested there and during February 1976, 435 adults and 20 chicks were present. Sixty-five gulls populated the island during 1974–1975, but only 22 during February 1976. They congregated around the pond during high tide, even when the terns were not nesting there (Hulsman 1977a).

METHODS

I observed the colony of terns from clumps of trees 10–40 m away during December 1974 and January 1975. I watched a group of 12 chicks standing on the beach from a dinghy anchored 10–20 m offshore during February 1976. In each case, I observed the birds for two 3- to 4-h periods daily. These watches were at least 2 h apart. My observations totaled 228 h over 36 days during 1974–1975 and 81 h over 14 days during 1976.

METHODS USED TO CHARACTERIZE PREY

I visually estimated the length and recorded the type of fish that terns brought into a section of the colony. In addition, I catalogued the number of successful and unsuccessful attempts of gulls to steal fish and the robbing methods that they used. Situations in which several gulls simultaneously tried to steal the same fish from a tern were considered one attempt. I was unable to identify and/or estimate the length of only 10.2–16.0% of the prey stolen by gulls during the observation periods in my study.

I estimated the length of each fish on the basis of bill length of the bird that was carrying it. Preliminary work with an injured Crested

TABLE 1. Relationships between the total length and weight in each of seven types of prey. The equations are of the form $W = 10^{(bL + a)}$ in which W is weight (g) and L is total length (mm).

Type of prey	Slope (b)	Intercept (a)	*r*	df	*P*
Exocoetidae	0.009	+0.007	0.999	5	0.0000
Monacanthus	0.016	−0.574	0.911	14	0.0000
Scombridae	0.010	−0.124	0.971	8	0.0000
Pomacentridae	0.013	−0.113	0.989	41	0.0000
Blenniidae	0.012	−0.135	0.973	6	0.0000
Gobiidae	0.087	+0.017	0.955	19	0.0000
Labridae	0.005	+0.777	0.683	20	0.0005

Tern indicated that I underestimated the total length of the fish, but overestimated its standard length (= the tip of the snout to the end of the last vertebra).

Fish were identified while they were being carried by terns. Coral reef fish have distinctive shapes and colorings and can be readily identified to family. In some cases, species such as sardines, anchovies, and atherinids, however, could only be positively identified in the hand and I therefore lumped them into a single group, which I termed "Silver" species. Some pelagic species of fish could be identified on the basis of their fins. Exocoetids (flying fish), for example, were identified by their elongated pectoral fins and heterocercal tails, and scombrids (tuna and mackerel) by the shape of their anal scutes and tails. Regurgitations were collected from Crested Tern chicks to verify the identity of some prey.

I estimated the weight of fish brought into the colony by means of allometric equations describing the relationship between the length of a fish and its weight (Table 1). I determined these relationships by using whole fish from regurgitated meals of tern chicks and specimens that a colleague and I speared.

DETERMINING PREFERENCES

I determined the gulls' preferences for fish of specific lengths by comparing, for each type of fish, the number in a length class stolen with the number of that length available to the gulls, i.e., carried into the colony by terns. Fish of a given length were "selected" or preferred by gulls when the proportion stolen exceeded their proportion of the available fish. Stolen and available fish were regarded as two distinct populations when proportions were calculated. The number of fish of species "a" and length "b" stolen (or available) was expressed as a proportion of the total number of species "a" of all lengths in the stolen (or available) population. For example, during December, fish 12–14 cm long constituted 10% of Silver spp. available to gulls and 26% of the Silver spp. stolen. Thus, gulls selected Silver spp. 12–14 cm long during December. Fish of a specific length class were "avoided" by gulls whenever the proportion stolen was less than the proportion available. For example, during December, fish 8–10 cm long constituted 23% of Silver spp. available, but only 10.5% of the Silver spp. stolen. Thus, gulls avoided Silver spp. of this length. Fish of a specific length class were neither selected nor avoided when the proportion stolen equalled the proportion available. The terms do not necessarily imply that a predator actively selected or avoided fish of specific sizes because robbing success affects the proportion of prey stolen.

I used a three-way G-test to examine the possibility that the shape of a fish influences the robbing behavior of Silver Gulls independently of the fish's length or the gull's robbing success. Fish were classified as disc-like or cone-like, according to their shapes. Disc-like fish, such as pomacentrids and monacanthids, are deep-bodied with respect to their lengths, whereas cone-like fish, such as engraulids and exocoetids, are narrow-bodied with respect to their lengths.

Some length classes were pooled for the test because fewer than 20% of the cells had an expected frequency ≥ 1 but <5 (see Siegel 1956: 110). Data from February 1976 were not analyzed because more than 20% of the cells had an expected cell frequency of <5 when pooled into the same classes that were used to analyze the data collected in December and January.

ROBBING METHODS

The methods that gulls use to steal food have been described previously (Hulsman 1976), but are included here for clarity. They are broadly divisible into "ground attakcs" (victim on the ground) and "aerial attacks" (victim in the air). Ground attacks include:

Hover-dives: A gull hovers above its victim on the ground and dives at it or at the fish it is carrying. The victim is usually an adult;

Walk-across-grab: A gull walks or runs to a tern and grabs the fish it is carrying. Aerial attacks involve:

Hover-chases: A gull hovers over its victim on the ground and then pursues it when it takes flight;

Chases: one or more gulls pursue the victim until it drops or swallows the fish it is carrying, or successfully escapes;

Underpasses: a gull attacks its victim in flight from behind and below and seizes the fish dangling from its mouth;

Jump-grabs: a gull on the ground jumps at a low-flying victim and tries to snatch the fish it is carrying.

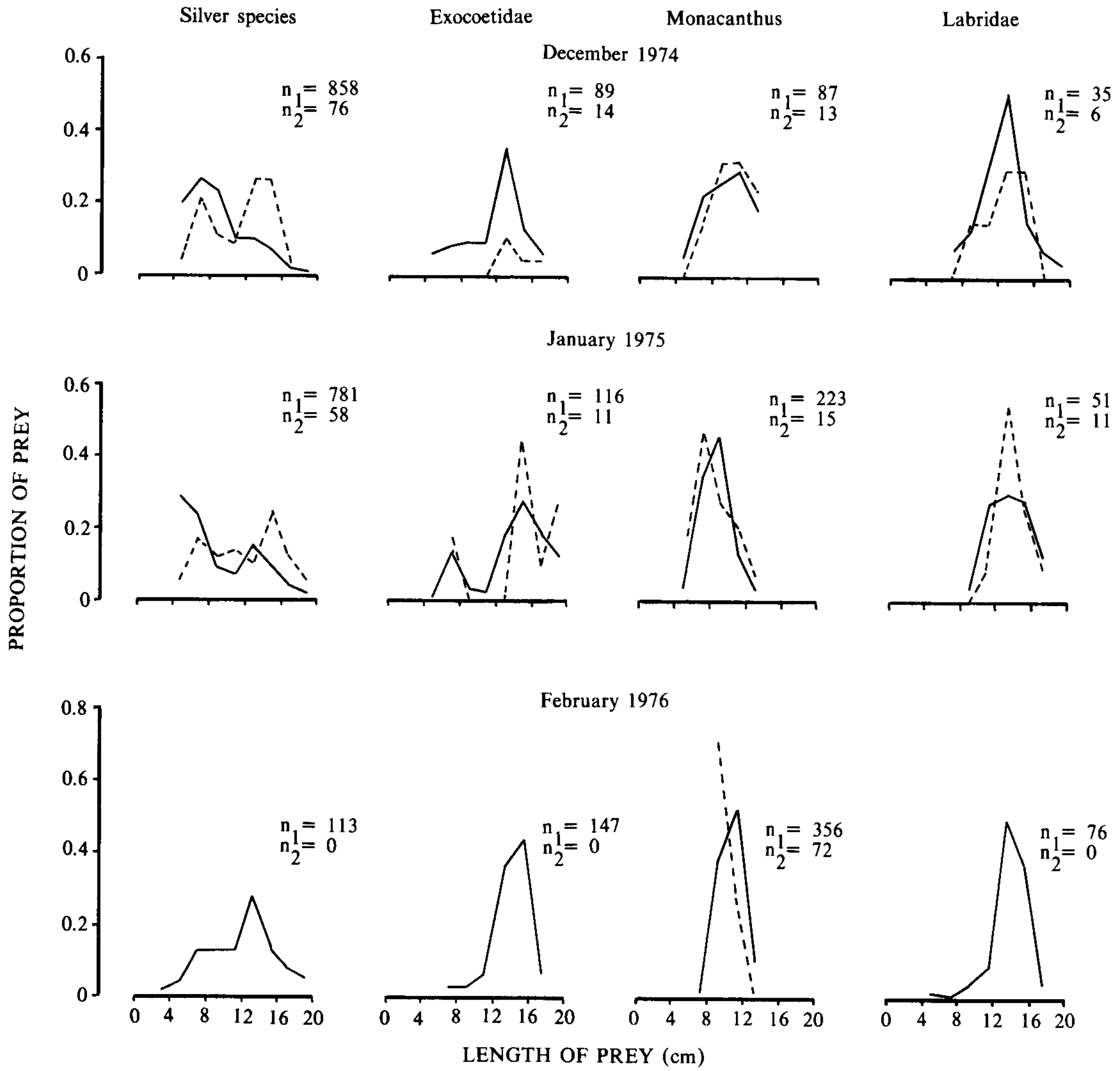

FIGURE 1. Proportions of four types of prey in each length class available to and stolen by Silver Gulls from Crested Terns during each of the three observation periods.

$$\text{Proportion available} = \frac{\text{No. of species 1 of specific length available}}{\text{Total no. of species 1 of all lengths available}}$$

$$\text{Proportion stolen} = \frac{\text{No. of species 1 of specific length stolen}}{\text{Total no. of species 1 of all lengths stolen}}$$

Available prey (——), prey stolen (- - -); n_1 is the number of available prey, n_2 is the number of stolen prey.

I had insufficient data to examine interactions between each of the above seven robbing methods and the shape and length of prey stolen using a *G*-test. I therefore lumped the methods into ground and aerial assaults for analysis.

RESULTS

LENGTH, WEIGHT AND TYPE OF PREY

The gulls' preference for fish of specific length changed over time (Fig. 1). For example, during December the birds preferred Silver spp. 12–18 cm long, during January they preferred fish 8–12 and 14–20 cm long, and during February they avoided Silver spp.

Although none of the fish carried by terns were too large to steal, Silver Gulls made fewer attempts to take the largest specimens than to take smaller ones. This was well illustrated by the frequency with which they attempted to steal Silver spp. and exocoetids of various sizes. For fish under 18 and 16 cm, respectively, the number of robbing attempts was directly re-

TABLE 2. Summary of chi-square analyses testing the hypothesis that Silver Gulls steal the same proportion of fish in each length class. Degrees of freedom (df) = $k - 1$ where k is the number of length classes of each type of fish.

Prey type	Month	Year	χ^2	df	*P*
"Silver" spp.	Dec.	1974	84.576	6	<0.001
	Jan.	1975	53.782	6	<0.001
Exocoetidae	Dec.	1974	7.664	2	<0.01
Monacanthus	Dec.	1974	0.277	1	>0.5
	Jan.	1975	2.776	2	>0.1
	Feb.	1976	40.718	2	<0.001
Arothron	Jan.	1975	1.063	1	>0.05
Reef	Dec.	1974	0.628	2	>0.5
	Jan.	1975	12.079	3	<0.01
Scombridae	Dec.	1974	0.977	1	>0.10
Carangidae	Dec. & Jan.	1974/75	0.012	1	>0.9
Pomacentridae	Dec. & Jan.	1974/75	6.151	3	>0.05
Blenniidae	Dec. & Jan.	1974/75	2.581	2	>0.1
Gobiidae	Dec. & Jan.	1974/75	1.825	3	>0.5
Labridae	Dec. & Jan.	1974/75	3.046	3	>0.1

lated to the length and weight of the fish. At times, gulls sought prey of specific length or weight (Table 2), but their preferences were also influenced by the availability of fish of various sizes.

AVAILABILITY OF PREY

Gulls appeared to select prey on the basis of their availability in some cases, but not in others (Fig. 2). During December, they selected prey types like exocoetids, blennies and gobies, which were less common than Silver and Reef species. They had fewer types of preferred fish during January than during December; and markedly preferred monacanthids during February.

During January and February, the most common prey species was the one most preferred by gulls. During January, for example, the main fish collected by Crested Terns was the tetraodontid *Arothron stellatus,* which was also the most preferred prey of gulls, whereas the monacanthid *Monacanthus filicauda* was not common and was little used (Fig. 2). However, in February, *M. filicauda* was not only the most common fish, but also the one most preferred by the gulls. Similarly, as the number of available *Arothron* relative to Silver spp. increased, so did the numbers of *Arothron* relative to Silver spp. stolen ($r_s = 0.6818$, 9 df, $P < 0.05$).

In some cases, the availability of a prey type influenced the likelihood that it would be stolen by gulls. In other cases, however, the length of a species precluded its use even though it was available in large numbers, as can be illustrated in terms of the gulls' preference for Silver species. Terns commonly brought Silver spp. into the colony, but the fish were of lengths (4–8 cm) avoided by gulls (Fig. 1); consequently, gulls did not steal them (Fig. 2).

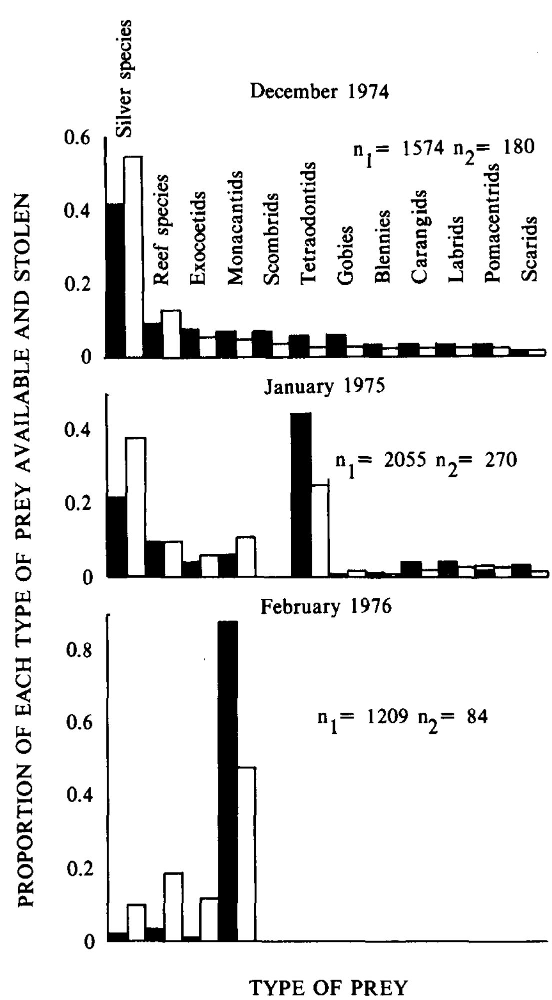

FIGURE 2. Proportion of each type of prey available (shaded) to gulls and the proportion of each type of prey actually stolen (unshaded) by them during each of the three observation periods. n_1 is the number of available prey, n_2 is the number of prey stolen. See Figure 1 for definitions of the "proportions" available and stolen.

TABLE 3. Spearman's rank order correlation (r_s) between the number of attempts that Silver Gulls made to steal fish and the length of the fish.

Prey type	n	r_s	P
"Silver" spp.	92	0.5567	<0.001
Exocoetidae	57	0.4439	<0.001
Monacanthidae	39	0.5409	<0.001
Tetraodontidae	60	0.3339	<0.01
Reef spp.	40	0.3207	<0.05
Scombridae	26	−0.0425	<0.9
Carangidae	33	0.0920	<0.9
Pomacentridae	30	0.1713	<0.4
Blenniidae	23	0.1446	<0.9
Gobiidae	17	−0.1853	<0.5
Labridae	22	0.0469	<0.9

TABLE 4. Spearman's rank order correlation (r_s) between robbing success and the length or weight of a fish.[a]

		Correlation coefficients between robbing success and	
Prey type	n	Length of prey (mm)	Weight of prey (g)
"Silver" spp.	73	−0.0494	...
Exocoetidae	44	0.3310*	0.3310*
Monacanthidae	28	−0.0800	−0.1080
Tetraodontidae	51	0.1258	...
Reef spp.	26	0.1374	...
Scombridae	24	−0.0065	0.1503
Carangidae	27	0.6129***	...
Pomacentridae	26	0.1674	0.3743
Blenniidae	17	0.1546	0.1546
Gobiidae	19	−0.1122	−0.1122
Labridae	21	−0.1793	−0.1387

[a] Correlation coefficients followed by asterisks are statistically significant at the 0.05 (*) or 0.001 (***) levels. Other coefficients are not significant ($P > 0.05$).

EFFECTS OF PREY SIZE ON THE INCIDENCE OF ROBBING ATTEMPTS

For five of the 11 types of prey that I studied, the number of robbing attempts increased with the length or weight of the fish within limits (Table 3). For the remaining six types of prey, I found no such relationship, i.e., gulls did not attempt to steal fish of one length (or weight) class more often than fish of other lengths or weights ($P > 0.05$, Kruskal-Wallis, one-way analysis of variance with 3–5 df for each type of fish).

ROBBING SUCCESS AND LENGTH OR WEIGHT OF PREY

Success of robbing attempts increased with the length (or weight) of prey type only in exocoetids and carangids (Table 4), and differed between some length classes of Silver spp. ($H = 15.13$, 7 df, $P = 0.032$). It was not significantly related to length in the other eight types of prey ($H \leq 6.742$, 3–4 df, $P > 0.05$). In general, robbing success was directly related to the weight of the fish (Fig. 3) because, on average, more robbing attempts were directed at large fish than at small ones.

SHAPE OF FISH

The results for December and January were similar in that length of prey was strongly associated with its shape (Table 5). The results for these months differed, however, in two ways. First, shape of fish and outcome of a robbing attempt were independent of each other during December, but not during January. Second, the outcome of a robbing attempt was significantly related to the shape and length of prey during December, but not during January. That is, in December, the degree of association between the outcome of a robbing attempt and length of a prey item varied with its shape (Fig. 4). Gulls strongly preferred disc-like fish during February, when they stole only four cone-like fish.

Most of the disc-like fish stolen during all three observation periods were 8–10 cm long. On the other hand, most of the cone-like fish stolen during December and January were 14–16 cm long (Fig. 4).

That shape of prey influences the outcome of a robbing attempt is also indicated by the significant difference ($t = 2.138$, 41 df, $P < 0.05$) between the regression equations describing the relationships between weight of prey and the proportions of disc- and cone-like fish stolen by gulls (Fig. 3). The proportion of available disc-like fish stolen by gulls increased with weight of fish at a faster rate than

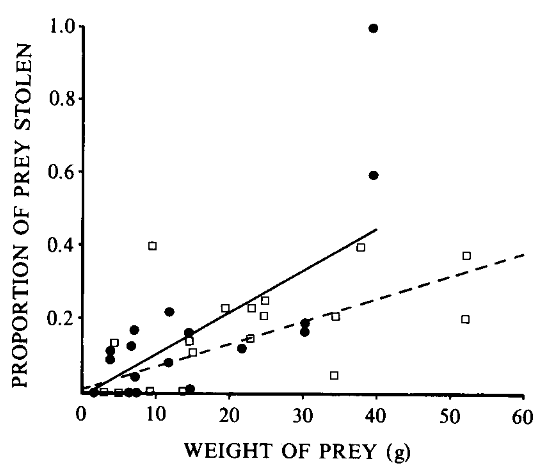

FIGURE 3. Proportion (P) of disc-like (black spot, solid line) and cone-like (white square, broken line) fish stolen by Silver Gulls as a function of the fish's weight (W). Both relationships are linear ($P < 0.001$) and described by the following equations: Disc-like: $P = 0.0146\ W - 0.0501$; Cone-like: $P = 0.0062\ W + 0.0085$. See Figure 1 for definition of "proportion of prey stolen."

TABLE 5. Results for tests of independence (*G*-test) of shape, outcome of a robbing attempt, and length of fish available to gulls during December 1974 and January 1975.

Hypotheses tested	December			January		
	df[a]	*G*[a]	*P*	df	*G*	*P*
Shape × outcome (independent)[b]	1	1.850	>0.05	1	32.714	<0.001
Shape × length (independent)	5	144.930	<0.001	6	519.024	<0.001
Outcome × length (independent)	5	59.642	<0.001	6	54.626	<0.001
Shape × outcome × length (interaction)	5	41.204	<0.001	6	−8.328[c]	>0.05
Shape × outcome × length (independent)	16	247.626	<0.001	19	598.036	<0.001

[a] The *G* statistic and its degrees of freedom are additive. If the number of categories of shape is "a," outcome "b," and length "c," then the degrees of freedom of shape × outcome × length (independent) = abc − a − b − c + 2; shape × outcome (independent) = ab − a − b + 1; shape × length (independent) = ac − a − c + 1; outcome × length (independent) = bc − b − c + 1; and shape × outcome × length (interaction) = (a − 1)(b − 1)(c − 1).
[b] Independent refers to the null hypothesis that there is no association between the specified variables.
[c] Negative interactions are possible.

did the proportion of cone-like fish. Moreover, as Figure 4 shows, gulls consistently stole more of the available disc-like fish than the available cone-like ones.

The number of times that gulls tried to steal a particular type of fish was a function of the latter's weight irrespective of its shape (disc-like: $r_s = +0.2404$, 125 df, $P < 0.01$; cone-like: $r_s = +0.2895$, 124 df, $P < 0.001$). Unfortunately, I cannot compare the frequency with which gulls tried to steal disc- and cone-like fish of the same weight because the results of my parametric and nonparametric regression analyses are not consistent with one another. However, I was able to compare the probability that a gull would try to take a disc-like fish with the probability that it would try to take a cone-like fish of the same weight (Fig. 5). Neither the slopes nor the intercepts of the regression equations describing the lines in Figure 5 differ significantly ($P > 0.05$, 25 df). In other words, it was equally probable that a gull would try to steal a disc- or cone-like fish of any given weight.

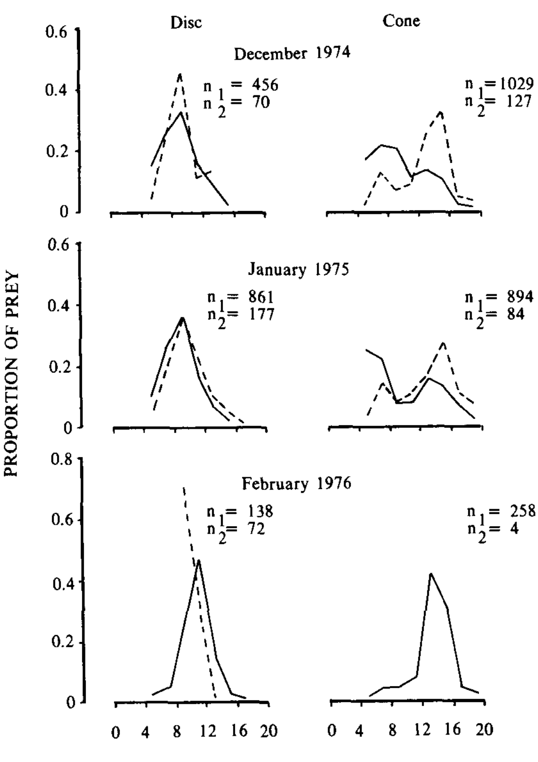

FIGURE 4. Proportion of disc-like and cone-like fish available (solid line) to and stolen (broken line) by Silver Gulls from Crested Terns during each of the three observation periods as a function of the fish's length. Refer to Figure 1 for definitions of the "proportions" available and stolen. n_1 is the number of prey available, n_2 is the number of prey stolen.

ROBBING METHODS

Neither shape nor length of prey alone influenced the robbing methods of the gulls, judging

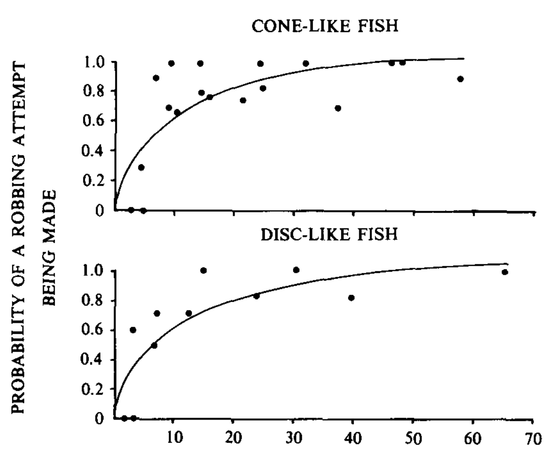

FIGURE 5. Relationship between the probability (*P*) of a robbing attempt and the specific weight (W) of a fish, for fish of two different shapes. The relationships are statistically significant ($P < 0.002$ and $P < 0.001$, respectively) and described by the following equations: disc-like fish: $P = 0.589 \log_{10} W + 0.03$; cone-like fish: $P = 0.605 \log_{10} W + 0.019$.

TABLE 6. Frequency with which fish of various shapes and lengths were stolen from terns with respect to the robbing method used by gulls. Data from each of the three observation periods were pooled.

Shape of prey	Robbing method	Number of prey stolen of length (cm) 4–8	>8–10	>10–12	>12–14	>14–16	>16–20	All lengths
Disc	Ground	11	38	22	15	6	1	93
	Aerial	15	51	26	8	1	0	101
	Both	26	89	48	23	7	1	194
Cone	Ground	8	3	10	16	18	7	62
	Aerial	10	6	9	28	30	9	92
	Both	18	9	19	44	48	16	154

by data for the entire study (Tables 6 and 7). Robbing method was, however, significantly related to the length *and* shape of prey, i.e., the degree of association between robbing method and shape of prey varied with the latter's length. Classifying the robbing methods simply as ground or aerial attacks masked possible differences between the frequency with which *particular* methods were used successfully by gulls. Nevertheless, I tested the association between a prey's shape and each robbing method, making the assumption that the prey's length had a negligible influence on the robbing method. Pairwise comparisons indicate that the shape of prey, robbing method, and the outcome of an attempted robbery were dependent on one another (Table 8). These factors also interacted significantly, i.e., the degree of association between the outcome of an attempt and the robbing method used by a gull varied with the prey's shape. (Table 9).

In their robbing attempts, gulls did not restrict themselves to seizing fish. During chases, for example, they frequently (52% of 87 cases) seized the tern and fell to the ground with it; and only then did they snatch the fish from it. In other chases, gulls collided with terns with such force that the latter were literally knocked out of the air (41% of 87 cases). In still other cases, gulls grabbed a tern's tail or wing in their bill before stealing the fish.

Some gulls used the vocalizations between adult terns and their chicks as cues in selecting potential victims. An incoming tern locates its chick in a colony by calling to it and homing in on its replies. Gulls followed chicks, which had answered incoming terns, in 6.8% of the thefts during February 1976 ($n = 340$). One or more gulls stood within 2 m of a chick and followed it whenever it moved away from them. When a parent tried to land and feed its chick, the gull(s) tried to steal the fish and was usually successful. Adults were, however, able to feed their young, when gulls were distracted by another tern nearby.

METHOD OF EVASION AND SUCCESS

Gulls were most successful when stealing from terns that were distracted. For example, 98.3% ($n = 60$) of those that attacked a tern as it was landing, or after it had just landed, were successful; in contrast, only 80.4% ($n = 46$) succeeded when terns had time to escape. Gulls did not fare nearly as well (5.3% success, $n = 33$) if a tern stood its ground and shielded its chick while threatening the pirate(s) overhead; or merely threatened a gull that was hovering overhead (17.7% success, $n = 62$); or attacked it (26.7% success, $n = 30$). Within limits, the farther a tern moved away from its chick while the latter was swallowing a fish, the greater the likelihood of robbing success.

DISCUSSION

Silver Gulls at One Tree Island attempted to steal fish of specific length (or weight). Preferred length varied with the type of prey and was not always the largest. In this respect, my results are like those of Dunn (1973), but contrary to those of Hopkins and Wiley (1972),

TABLE 7. Summary of results of tests of independence (*G*-test) of robbing methods used by gulls, and the shape and length of fish that they stole. Data analyzed are in Table 6. Refer to Table 5 for explanation of df.

Hypotheses tested	df	*G*	*P*
Method × length (independent)	5	0.750	>0.05
Method × shape (independent)	1	2.054	>0.05
Length × shape (independent)	5	142.536	<0.001
Method × length × shape (interaction)	5	12.662	<0.05
Method × length × shape (independent)	16	158.002	<0.001

TABLE 8. Number of successful and unsuccessful attempts by gulls to steal disc- and cone-like fish with respect to their robbing method. Results from each of the three observation periods were pooled.

	Number of attempts to steal					
	Disc-like fish			Cone-like fish		
Robbing method	Successful	Unsuccessful	Total	Successful	Unsuccessful	Total
Hover-dive (directed at an adult tern)	58	37	95	57	32	89
Hover-dive (directed at a tern chick)	24	4	28	2	1	3
Walk-across-grab	11	18	29	3	57	60
Hover-chase	17	2	19	20	7	27
Chase	49	155	204	38	127	165
Underpass	17	12	29	23	32	52
Jump grab	18	25	43	11	11	22
Combined	194	253	447	154	267	421

who found that the most common targets of pirates were terns carrying the largest fish. Perhaps gulls try to steal fish with the highest net energy content, and in the situations observed by Dunn (1973) and me the net energy gained from the largest fish was less than that gained from a slightly smaller one. In the situation observed by Hopkins and Wiley (1972), perhaps the largest fish had the highest net energy yield. If gulls select a prey item on the basis of its energy content, the weight of a fish's edible parts is important. Nonetheless, gulls may not respond directly to weight of a prey item, but instead to some indicator of weight such as length or size. For example, Dunn (1973) found that in cases where two prey species of the same length differed in weight, pirates stole more of the heavier species. Pirates may use overall size when selecting potential prey, size being defined by the latter's overall dimensions, i.e., its length, breadth, and depth. Certainly shape is important since gulls discriminate between disc- and cone-like fish (Fig. 3). Indeed, the width or depth of a fish often limits the size of prey eaten by terns and gulls more than its length does. A tern or gull cannot, for example, swallow a fish if the prey is too wide or deep for its gape, even though the fish may be shorter than the bird's esophagus (Hulsman 1981). Therefore, the largest disc-like fish that a tern or gull can swallow is shorter than the largest cone-like fish that it can swallow.

Gulls consistently stole more of the available disc-like than cone-like fish, and they were more successful in taking this shape of fish from terns. A fish's length must also be important because gulls tried to steal fish of some length classes more often than fish of other classes. Shape and length of prey were significantly associated with one another during December (Table 5), when gulls strongly preferred disc-like fish 8–10 cm long and cone-like fish 14–16 cm long. Furthermore, in three types of fish (Table 4) robbing success was directly related to the length (or weight) of the prey. Dunn (1973) found, however, that the robbing success of Roseate Terns (*S. dougallii*) decreased with increasing length of fish. He suggested that terns carrying large fish were more vigilant and so better prepared to evade pirates. The difference in the relationship between robbing success and length of fish for Silver Gulls, on one hand, and Roseate Terns, on the other, is probably related to differences in their robbing methods (Hulsman 1976). Silver Gulls stood in the terns' colony and persistently attempted to steal fish from birds that were on the ground or trying to land. Roseate Terns, on the other hand, made brief "all-or-nothing" attempts to steal fish from terns flying to their colony. Instantaneous attempts are more readily evaded by a victim than attempts that last more than several seconds.

The gulls' methods differed in success. The

TABLE 9. Summary of results of tests of independence (G-test) of robbing method, outcome of a robbing attempt, and shape of prey. Data are in Table 8. Refer to Table 5 for explanation of df.

Hypotheses tested	df	G	P
Outcome × method (independent)	6	52.530	<0.001
Outcome × shape (independent)	1	4.206	<0.05
Method × shape (independent)	6	54.324	<0.001
Outcome × method × shape (interaction)	6	130.104	<0.001
Outcome × method × shape (independent)	19	241.164	<0.001

most successful were Hover-dives and Hover-chases, the least successful were Walk-across-grabs (directed at cone-like fish) and Chases. That Hover-dives and Hover-chases were highly successful was probably because terns do not maneuver well on the ground, and they are preoccupied while displaying and looking for, or offering, fish to their chicks. This would enable gulls to get into an advantageous position from which to launch a robbing attempt. By the time a tern saw them overhead, it would either be unable to escape or would be easily caught before it flew more than a few meters (hence the success of Hover-chase). Chases were not very successful because terns can outmaneuver and evade gulls in flight. Terns are also probably more alert while flying than when on the ground among other terns. As I expected, gulls using Hover-dive and Walk-across-grab were more successful in stealing disc-like fish than cone-like ones, probably because terns must handle deep-bodied fish for such a long time that pirates are able to position themselves advantageously for a robbing attempt (see Gochfeld and Burger 1981). Carangids, for example, have deep bodies and were stolen most often from chicks or adults that were offering them to chicks. These fish are commonly so deep-bodied that tern chicks (and even adult gulls) have difficulty swallowing them. The combination of the depth and weight of these fish increased the time required to handle them. When a pirate tried to steal such a fish, the chick usually dropped it and it was stolen in the resulting confusion.

Two conflicting selection pressures probably determine the size of fish that terns carry into their colonies—the need to provide chicks with adequate amounts of food and the need to minimize loss of fish to pirates. It is in a tern's interest to make as few fishing trips as possible, thereby reducing the amount of time and energy spent flying to and from the colony. To do this, a tern should collect prey that provide the highest net energy to the young. However, if fish of such size are more easily stolen than fish of other sizes, then a tern must compromise. (I assume that gulls would steal so many fish of the optimal size that a tern chick would consume less energy from them than it would obtain from smaller fish). A tern would learn through trial-and-error which prey were the most economical for itself and its chick when robbing pressure is high.

In conclusion, it appears that gulls respond to several cues about a fish's size when they try to steal it from a tern. The shape of the fish is important because it affects the perceived size of the fish. Gulls may select prey on the basis of its overall dimensions (length, breadth, and depth) and/or ratios of these dimensions. Robbing success differs with the length of some types of fish, but not others. The relationship between the outcome of a robbing attempt and the robbing method used by a gull varies with the shape of the prey. Robbing success is also affected by the maneuverability of terns, their methods of evasion, and the speed with which they react to gulls.

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