

## NONRIGOROUS FORAGING BY ROBBING EGRETS<sup>1</sup>

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**Abstract.** The premise that a species will maximize its net energy intake over the short term was tested by studying the robbing behavior of the Great Egret. In wading-bird feeding aggregations of the southern Florida Everglades, the 5 most common species robbed other birds, and this behavior consumed 10% of the feeding time of the Great Egret. When an egret robbed other birds, it got larger prey, but it took longer, caught fewer prey, and expended more energy than it did feeding in more typical fashion by slow walking or standing. Nonrobbing behavior had a gross energy intake per time  $3.1\times$  greater than robbing. The cost-benefit ratio of robbing was 70% larger than for standing feeding. The combined use of both standing feeding and robbing resulted in a cost-benefit ratio 10% larger than for standing feeding alone. The use of a nonoptimal behavior is interpreted to suggest that energy return need not always be optimized over the short term. Minimizing cost-benefit ratios, optimizing time budgets, or maximizing net energy gain may occur only intermittently during an animal's annual cycle. The existence of a less-than-optimal behavior within the egret's foraging repertoire suggests that, under circumstances other than those studied, it might contribute to foraging optimization. It is predicted that an animal should attempt to capture each prey that it encounters when the occurrence of a prey item is a relatively rare and random event and if the potential penalty were small. Under these conditions, which would occur during periods of nonrigorous foraging, an animal can use a nonoptimal behavior.

**Key words:** *Aves*; *Casmerodius*; *cost-benefit*; *energy optimization*; *Everglades*; *feeding*; *Florida*; *foraging ecology*; *Great Egret*; *kleptoparasitism*; *nonrigorous foraging*; *optimal foraging*; *optimization*; *prey robbing*; *wading birds*.

### INTRODUCTION

The proposition that natural selection produces optimal phenotypes is nearly tautological. Because of this, and the ease of solving mathematical models for minima or maxima, optimization models have been used with apparent success to predict evolutionary solutions to problems of maximizing fitness. Such evolutionary models also have been applied directly to real-time ecological problems under the assumptions (1) that optimal solutions exist, and (2) that they mimic or are similar to those achieved over evolutionary time (Cody 1974). Foraging ecology and niche breadth are often targets for optimization studies because of their tractability in the field and because of the easily accepted argument that energy optimization should be directly relevant to evolutionary fitness. MacArthur and Pianka (1966), Emlen (1966), Schoener (1971), Cody (1974), Pulliam (1974), Katz (1974) and others have approached from various perspectives the problem of strategic optimization of foraging ecology. At the heart of such approaches is the premise that organisms must act optimally, because if they did not they would be selected against. This permits the testing of optimization models in the real world by observing how closely an organism's behavior actually approaches the theoretical optimum set for it.

However, it has not been proved adequately that animals always optimize costs and benefits over the short term as would be required for testing most evolutionary models. This paper reports on an attempt to test this assumption by analysis of energetic optimi-

zation of foraging behavior among wading birds (Ciconiiformes). The behavior studied was the Great Egret (*Casmerodius albus*) robbing prey from herons, egrets and ibises, with which it forages in mixed-species aggregations (Kushlan 1976a). Great Egrets typically forage by waiting for prey to approach and so would appear to follow a strategy of energy maximization. I tested the hypothesis that Great Egrets maximize their net energy intake by enlarging their behavioral repertoire to include prey robbing. This was studied by determining the relative costs and benefits of prey robbing as contrasted with the egrets more typical stand-and-wait foraging behavior.

### METHODS

Data were collected during a week in February 1976 at locations in the Everglades of southern Florida where wading birds gathered in mixed-species feeding aggregations. The 20 aggregations studied included as many as 7 species, with White Ibis (*Eudocimus albus*) and Great Egrets being the most abundant (Table 1). Wood Storks (*Mycteria americana*), Great Blue Herons (*Ardea herodias*), and Little Blue Heron (*Florida caerulea*) occurred frequently, but Snowy Egrets (*Egretta thula*) and Roseate Spoonbills (*Ajaia ajaja*) participated in the aggregations relatively infrequently. Data were gathered in 607 independent 1-min observations of the entire feeding aggregation, and 20 counts of aggregation composition. Birds to be observed were selected randomly and watched for 1 min at a time, after which another bird was chosen for observation. For each minute, a foraging ethogram was constructed showing the frequency and duration

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TABLE 1. Number of individuals of various species comprising the feeding aggregations ( $n = 20$ )

Taxa	Mean number per aggregation	Percentage of total	Percentage frequency occurrence
Great Egret	73	37	100
White Ibis	62	31	100
Little Blue Heron	40	20	100
Wood Stork	14	7	100
Snowy Egret	5	2	5
Great Blue Heron	4	2	100
Roseate Spoonbill	1	1	10

of the bird's activities and the success of attempted prey capture or prey robbing. Prey taken or pursued were identified and their length estimated to the nearest centimetre. Length data were converted to energy content using empirical length-weight data and energy content values of prey were determined with a Parr<sup>®</sup> adiabatic calorimeter. Data are given  $\pm$ SD and carried to 1 decimal place beyond measurement precision for purposes of comparison. Names of feeding behaviors follow Kushlan (1976b).

RESULTS

*Prey robbing in the aggregation*

All 7 species of wading birds in the aggregation robbed other birds. For the 5 species most frequently present, Wood Storks, Great Blue Herons, and Great Egrets each robbed White Ibis and Little Blue Herons, and White Ibis robbed Little Blue Herons (Table 2). Great Blue Herons robbed Great Egrets and all, except Wood Storks, robbed individuals of their own species. As a generalization, a bird robbed conspecifics and individuals of smaller species (Fig. 1).

The incidence of robbing among the species differed significantly from the relative numbers of each species observed in the aggregations ( $\chi^2, p < .01$ ), implying that some species robbed disproportionately. Comparing occurrence with robbing incidence (percentage of total, Table 1 vs. Table 2) shows that Wood Storks, Great Blue Herons and Great Egrets robbed more and White Ibis and Little Blue Herons robbed less frequently than expected. Thus, robbing tendencies were greater in the larger birds, and there were more instances of Great Egrets robbing than for other species in the aggregations (Table 2).

TABLE 2. Observations of robbing in wading bird aggregations. Bird weight, as an index of size, is in parentheses (data from Palmer 1962)

Robber	Robbed					Total	Percentage of total
	WS	GBH	GE	WI	LBH		
Wood Stork (WS) (3.2 kg)	0	1	7	2	1	10	14
Great Blue Heron (GBH) (2.7 kg)	0	1	5	1	0	7	10
Great Egret (GE) (0.9 kg)	0	0	11	27	9	47	65
White Ibis (WI) (0.8 kg)	0	0	0	4	2	6	8
Little Blue Heron (LBH) (0.35 kg)	0	0	0	0	2	2	3

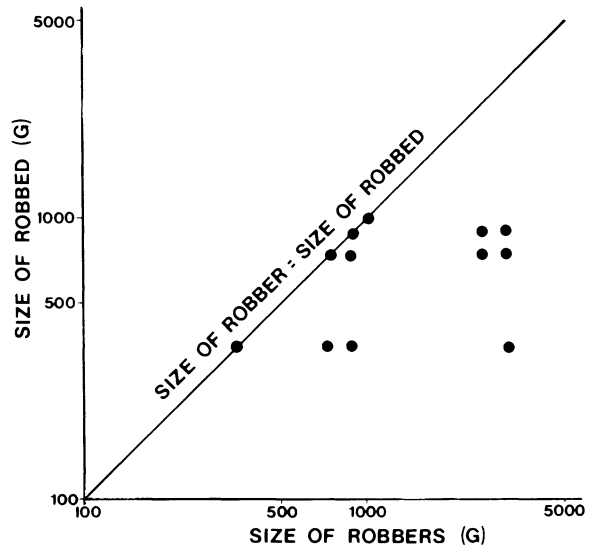


FIG. 1. Relation of size of bird to incidence of robbing, showing that individuals robbed bird species of similar or smaller size. Size of bird equated to weights shown in Table 2.

*Great Egret as a robber*

Prey robbing was both frequent and widespread among the larger species in the wading-bird aggregation and, because the Great Egret was the principal robber, its behavior was studied in detail. An average of 3% of the Great Egrets present were engaged in robbing during 1-min observations and each egret robbed about  $2\times$  per hour. A foraging egret stood within or waded slowly about the aggregation, often in an erect posture, apparently watching both the water and other birds. An egret would stalk a prey item it spotted or pursue another bird that had a prey item in its bill. Birds pursued were those with prey large enough to require a relatively long handling time in preparation for swallowing. The pursuing egret would walk quickly or fly toward or after the intended victim and attempt to force it to drop its prey. Thus robbing developed from standing feeding when a suitable opportunity became available.

The success and cost parameters associated with each foraging behavior are contrasted in Table 3. The size of prey taken by a Great Egret during robberies averaged significantly larger than those caught by a

TABLE 3. Relative costs and benefits of robbing and feeding alone

	Robbing	Standing-feeding	Both <sup>b</sup>
<b>Benefits</b>			
Energy content of prey	9.2 kJ	7.11 kJ	7.32 kJ
Catch rate per minute	0.01 prey	0.04 prey	0.037 prey
Gross energy return per minute	0.09 kJ	0.28 kJ	0.26 kJ
<b>Costs</b>			
Pursuit, handling time	0.5 min	0.082 min	0.12 min
Energy expenditure	10	1	1.9
Energy expenditure per minute	20.0	12.0	12.8
Cost/benefit <sup>a</sup>	222	43	49

<sup>a</sup> C/B = (Energy expenditure per minute) (energy return per minute).

<sup>b</sup> Because an egret spent 10% of its time robbing, totals for both behaviors = (.10) (rob) + (.90) (standing-feeding).

Great Egret when fishing by itself (*U*-test,  $p < .05$ ). From independent strikes, egrets caught prey ranging from 1 to 7 cm long, averaging  $3.5 \pm 1.5$  cm. The size of fish involved in unsuccessful robbery attempts was the same ( $3.8 \pm 0.8$  cm) as those Great Egrets caught on their own. Thus, egrets were more successful at robbing birds that had relatively large prey, because these required longer handling times by the victim, but were relatively unsuccessful with fish of the size that comprised their nonrobbing diet. About one fourth (27%) of the robbing efforts by Great Egrets were successful, whereas an egret feeding on its own captured prey successfully in 58% of its attempts. Because of the greater success, a Great Egret caught prey on its own at a rate of .04 prey/min but robbed at a rate of .01 prey/min.

The larger size of fish captured by robbing meant that the energy return was greater per prey item caught than for fishing alone (Table 3). The mean energy content of fish obtained by robbing was 9.20 kilojoules (kJ)<sup>a</sup>, whereas the energy content of fish caught by an egret feeding alone averaged 7.11 kJ. However, differences in the catch rate more than compensated for the differences in energy per prey. Thus the gross energy return was .09 kJ/min for robbing and .28 kJ/min for feeding alone.

The costs of robbing and attendant aggressive encounters were high in terms of both time and energy expenditure (Table 3). A Great Egret initiated a direct aggressive encounter on the average of 11.4× per hour or once every 5.25 min of feeding. Great Egrets directed 55% of these attacks at other Great Egrets and 31% to White Ibis. Encounters lasted from 3 s to 5.26 min, averaging 31 s each. Thus, on the average, a Great Egret spent ≈6 min of each hour or 10% of its feeding time in aggressive encounters and subsequent

<sup>a</sup> 1 kilocalorie = 4.184 kJ.

robbing activity. These encounters consisted of hopping, flying, supplanting attacks, grabbing at prey items and, often, long pursuit flights. The relative costs of the 2 behaviors can be estimated by using the relative costs of flying and the costs of caged existence metabolism as indices. Flying costs in several non-passerines are 12× standard metabolic rate (SMR) (Utter and LeFebvre 1970). Existence costs for the White Ibis are 1.3× SMR (Kushlan 1977). If these values hold for the Great Egret, flying is ≈10× more costly than existence metabolism. Thus, robbing may be estimated to be ≈10× more energy expensive than fishing by standing and waiting. Because each behavior had different time expenditure, to allow for comparisons, the relative costs of pure feeding of each type can be estimated by calculating the expenditure per minute of each type. This relative cost is 1.7:1 (i.e., 20:12, Table 3). These data permit the assessment of the relative energy benefits and costs of robbing and independent foraging. If egrets used only 1 or the other behavior, the cost-benefit ratio of robbing was 5.2× that of standing foraging (222/43, Table 3). A Great Egret had a lower cost-benefit ratio if it fed by standing only. Considering the mix of these behaviors used in the situation studied, the cost-benefit ratio of the mix was 1.1× that of standing foraging alone (49/43, Table 3). A Great Egret does not minimize its cost-benefit ratio by including robbing in its foraging repertoire. Nor, disregarding costs, does it maximize its gross energy intake by using a mixed strategy.

DISCUSSION

Even though prey robbing resulted in a Great Egret obtaining more energy per prey item, the lower success rate and greater time expenditure led to a lower gross energy intake. This, along with higher cost, made robbing less valuable energetically than the stand-and-wait method of prey capture generally used by the egret. The inclusion of this behavior in the Great Egret's feeding repertoire is not adequately explained by the hypothesis that it maximizes the egrets' net energy return. Nor will an egret faced with the choice of robbing or feeding alone minimize its cost-benefit ratio by engaging in robbing. Yet this seemingly nonoptimal behavior consumed 10% of the Great Egret's feeding time and was indulged in by all of the 5 most common members of the feeding aggregations studied, a frequency that suggests that it cannot be highly maladaptive in the context studied.

There are several alternative hypotheses concerning the energy budget of the Great Egret that might explain the existence of robbing. (1) By robbing, a Great Egret might minimize time expended in feeding. However, because the return per minute from feeding alone was 3× that of robbing, it would take 3× as long to obtain a given food ration by robbing. MacArthur (1972) suggested that a prey item should be added to

the diet if its pursuit time per prey gram (or energy value) were less than the mean pursuit and search time of previous items. If the previous diet were derived by standing only and the next item were available by robbing, then the pursuit time for that item would average 11.95 minutes/kilojoule as compared to 3.6 min/kilojoule for the previous standing diet (i.e., 1/0.09 kJ/min vs 1/0.28 kJ/min, Table 3). By MacArthur's (1972) criterion, the item available by robbing should not be added to the diet. (2) A Great Egret, by robbing, might minimize the risk of not obtaining any prey. This was not the case however, because the probability of obtaining a prey item was proportional to the success rate, which for robbing was half of that for standing feeding. (3) A Great Egret might enlarge its niche breadth of obtaining additional kinds or sizes of prey by robbing. However, identified prey species were taken by both methods, except for 1 species that was taken only by egrets feeding alone. Thus, robbing did not provide additional prey types. This result also precludes an egret's obtaining a particular nutrient available only in robbed prey items. Furthermore, the size range of prey taken by feeding alone fully encompassed the size range taken by robbing. If anything, robbing provided a smaller array of prey sizes. (4) Because optimization involves the entire time-energy budget of an organism, a Great Egret might use a behavior that sacrificed foraging effectiveness if doing so compacted the foraging bout and allowed time for other important behaviors. However, robbing did not increase the time available for other activities because it took longer and returned less than not robbing. None of these hypotheses adequately explains the existence of robbing behavior in the context of energy optimization.

Since the entire budget cannot be optimized when energy-wasteful behaviors are regularly included, it is reasonable to suggest that, at any given time, an animal may not have to optimize its time-energy budget. This is not to say that time-energy budgets never approach theoretical optimization. There are critical segments of annual cycles when net energy intake may approach a maximum, such as periods of intense resource-based competition, periods of high energy expenditure, and periods of food shortfalls. In the life of a temperate-zone bird, for example, optimization may be necessary to insure individual survival during winter food shortage and to insure reproductive success during nesting when energy demands are high. During such times, an individual no doubt optimizes its foraging behavior, and its relative ability to do so determines its genetic success. The severity of such periods will vary from year to year, and thus, so would the need for optimization. Therefore, net energy maximization may occur only periodically within an animal's annual or life cycle, while at other times, energy intake need not be maximized and in such periods foraging can be pursued nonrigorously. The premise of

full-time optimization of an animal's energy budget may well be an extreme expectation that in some circumstances surpasses that necessary for existence. In the current study, robbing occurred outside the breeding period at locations where food was highly available because of seasonal drying, as is typical of places where wading-bird aggregations form in southern Florida (Kushlan 1976a).

The results presented here differ from some other considerations of optimal foraging. While some studies have provided strong support for optimal foraging hypotheses (Kushlan 1973, Werner and Hall 1974, Gill and Wolf 1975, Charnov 1976), other results have been more equivocal (Rosenzweig and Sterner 1970, Smith and Dawkins 1971, Willson and Harmeson 1973, Smith and Sweatman 1974). Emlen and Emlen (1975) tested the ability of laboratory animals to feed in a maximally efficient fashion. The test animals did not behave as predicted and Emlen and Emlen (1975) interpreted their data as being consistent with the optimization hypothesis if allowance were made for imperfect decision making on the part of their laboratory mice. Alternatively, in light of the field-based data presented here, the Emlens' (1975) results could mean that the captive mice were required to forage only in a nonrigorous fashion.

Nonoptimal foraging behavior may be functional in a social rather than energetic context. Thus, robbing might be a way of socially dominating other birds. In the present case, this does not appear to be a deciding factor because feeding dominance among aggregated wading birds is established by size (Kushlan 1978), which generally requires only low-intensity agonistic responses toward birds intruding rather than intensive, energy-wasteful prey robbing. Alternatively, aggression associated with robbing might have sexual overtones. In the Great Egret, intraspecific robbing does not appear to function in sexual dominance or pair formation because, as far as is known, all mate selection occurs away from the feeding ground.

Another possibility is that robbing might represent spiteful behavior (Hamilton 1970). Spite requires recognition of and differential response to individuals having differing degrees of relationship (Wilson 1975). Individual recognition is improbable in the feeding aggregations studied because they were large, ephemeral, and constantly varying in membership. Thus, intraspecific robbing was probably not spiteful because, if there were no benefit, as required for spiteful behavior, harming an unknown bird affords no advantage either to the bird doing the harming or to its near relatives. In fact, however, robbing does supply a relative benefit to the robber compared with its victim (benefit/cost = .09/10:0/10 or .009 > 0—Table 3). Thus there is benefit to the robber and a cost associated with being robbed, and so it appears that robbing is merely another example of selfish rather than spiteful behavior. Viewed in this way, as exploitative com-

petition, robbing could deprive potential competitors of prey. Interspecifically, the heavy incidence of robbing appears to reduce the size of prey consumed by White Ibis. Intraspecifically, robbing might also deprive other egrets of prey. Such competitive prey reduction would also occur and, because of greater success frequency, at a higher rate than by an egret standing and feeding. Robbing, even if selfish, would still be energetically wasteful because of its low success rate.

It might be asked, then, why this behavior should persist at all? In the present study, I attempted to test the existence of short-term energy optimization by examining an animal's foraging tactics under a particular set of environmental circumstances, in which use of robbing behavior appeared contrary to expectations of optimal foraging. Possession of the behavioral plasticity to use such a behavior suggests that the apparently suboptimal behavior may indeed function to maximize energy gain under some different set of resource conditions. A fluctuating environment, such as found in the Florida Everglades, may be a factor in maintaining the need for various alternative feeding behaviors.

In a given circumstance, an animal's choice of a foraging behavior among all those maintained in its repertoire depends on how it tracks its environment and on its current need for optimizing feeding effort. In order to track its environment, an animal must use past prey events to generate some probability of the anticipated success, energy cost, and outcome of a given behavioral response to the next occurring prey event. In this context, the sporadic use of a nonoptimal behavior might be a way of gathering sufficient background data to permit prediction as to the proper behavioral response to a future prey event, although in the Great Egret's case, robbing appeared too frequent to be so explained. Prediction depends in part on the statistical distribution of prey events themselves. If the appearance of a potential prey item over a period of time was a relatively rare event and independent of other prey events, a bird's encounter with prey might be expected to follow a Poisson distribution, as indeed does the Great Egret's ( $\chi^2$ ,  $p < .005$ ,  $n = 60$ ). A bird tracking its environment under such conditions might therefore be expected to respond to each random and rare prey item, particularly an obvious one held in the bill of another nearby bird, as long as there was no severe penalty incurred for doing so. A secondary result might well be a direct reduction in prey available to competitors. The key consideration, however, is that excess costs not be debilitating. Such would be the case under those circumstances when foraging can be pursued nonrigorously, which may therefore result, over the short term, in the use of apparently nonoptimal feeding behaviors.

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