

$\min = 0.1X$ and the inequality becomes: $4.8 \text{ kJ/min} - X > 0.313 \text{ kJ/min} - 0.1X$ or $X < 4.99 \text{ kJ/min}$. Therefore it should rob if the cost of robbing is less than 4.99 kJ/min .

While the actual foraging costs are not available, they can be approximated using a form of Kleiber's (1975) metabolic equation: metabolic rate (MR) = $kW^{.756}$. Using a SMR (standard metabolic rate) value of 0.247 kJ/min for a 0.8-kg White Ibis (Kushlan 1977) and solving for k gives a value of 0.292 . Inserting this value back into the equation and solving for a 0.9-kg Great Egret gives a SMR of 0.27 kJ/min . If as Kushlan suggests, existence (i.e., stand-feeding) cost is $1.3X$ SMR and robbing (i.e., flight) cost is $10X$ existence cost, then the cost of stand-feeding is $(0.27 \text{ kJ/min})(1.3) = 0.35 \text{ kJ/min}$ and the cost of robbing is 3.51 kJ/min .

Therefore, insofar as these figures are accurate, egrets should rob opportunistically. Further, since the net return from stand-feeding is negative ($0.313 - 0.351$), egrets may at times be unable to maintain a positive energy balance while foraging from stand-feeding alone, but by robbing could overcome or at least reduce this deficit.

In summary, what Kushlan originally interpreted as a paradoxical case of nonoptimal foraging appears to be a complex feeding strategy that allows the egret successfully to take advantage of the opportunities presented by large mixed-species feeding aggregations. Egret foraging seems to be optimal as defined by current foraging theory, and rather than contradicting it, fits its predictions and provides an unusually good example of the heuristic value of the theoretical approach to feeding ecology.

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SHORT-TERM ENERGY MAXIMIZATION OF EGRET FORAGING¹

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I recently addressed the question of whether in a specific situation it was energetically effective for Great Egrets to enlarge their repertoire of foraging behaviors to include prey robbing (Kushlan 1978). This was studied by determining the relative costs and benefits of prey robbing as contrasted with the egrets' more typical standing foraging behavior. My main interest was to explore whether predictions of maximized foraging are independent of time scale. That is, whether energetically efficient decisions must always be made, even over short time periods. The results showed that an egret obtained more energy per time with less cost feeding by standing than by robbing. This demonstrated that prey robbing was an energetically ineffective behavior. I further analyzed the choice between behaviors in several ways, primarily by comparing gross energy intake and by combining foraging parameters in a cost/benefit (c/b) function. I concluded that "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" (Kushlan 1978).

Dunbrack (1979) suggests that a cost/benefit analysis would always show that a pure strategy is optimal. The answer depends on the question. The important question is not which single behavior is best but whether a behavior should be added to an existing repertoire. An animal should not add those behaviors that will adversely change the foraging function under consideration. Conversely, a more effective behavior should be added. The addition of robbing to a standing bout increased the cost/benefit ratio for the resulting mixed strategy (Kushlan 1978); therefore, to minimize a cost/benefit ratio, robbing behavior should not be added.

Analyses using relative costs, gross energy intake, and cost/benefit ratios avoid the need to fix exact energy values for various active behaviors of large wild birds. The uncertainty of such estimates may become particularly troublesome when used to calculate net energy value of a behavior which may appear to be negative because of an exaggerated cost estimate. Dunbrack (1979), however, proposed to follow this approach by comparing net energy per unit of pursuit and handling time (E_{net}/HT) as discussed by Pyke et al. (1977). He suggested that net energy per pursuit and handling time be calculated by subtracting costs from benefits using $[(P)(E_{\text{prey}})/\text{HT}] - (E_{\text{cost}})/\text{HT}$, where P is the probability of success. The pertinent benefit values for robbing are $P = 0.27$, $E_{\text{prey}} = 9.2 \text{ kJ}$, $\text{HT} = 0.517$ (Kushlan 1978).

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The gross energy return is $(0.27)(9.2 \text{ kJ})/0.517 = 4.8 \text{ kJ/min}$ (Dunbrack 1980). The equivalent benefit data for feeding by standing are $P = 0.58$, $E_{\text{prey}} = 7.11 \text{ kJ}$, $HT = 0.082 \text{ min}$ (Kushlan 1978). The gross energy return is $(0.58)(7.11 \text{ kJ})/0.082 \text{ min} = 50.3 \text{ kJ/min}$. This result is higher than the 0.313 kJ/min calculated by Dunbrack and leads to a complete revision of his subsequent conclusions. The calculated energy costs of each behavior (0.351 kJ/min for standing, 3.51 kJ/min for robbing) are subtracted to obtain E_{net}/HT . The net energy value for standing-feeding (49.9 kJ/min) is considerably greater than that for robbing (1.29 kJ/min). Robbing behavior would decrease the combined net energy intake per time of the expanded repertoire and, under the usual net energy optimization criterion, should not be added.

It may be useful to reconsider the cost/benefit analysis for the two behaviors using calculated metabolic estimates. $C/b_{\text{rob}} = (3.51 \text{ kJ/min})/(4.8 \text{ kJ/min}) = 0.73$; $c/b_{\text{stand}} = (0.351 \text{ kJ/min})/(50.3 \text{ kJ/min}) = 0.007$, or 104 to 1. The same results hold using relative costs of 10 to 1. By this analysis, robbing would raise the total cost/benefit function. To minimize the cost/benefit ratio, robbing should not be added to the repertoire.

Because a searching egret might be prepared to rob or to spend an equivalent amount of time continuing to search for, pursue and handle prey by standing-feeding, a pertinent analysis might be to compare the results of robbing to continued search and standing during the 0.517 min required to rob. First, a clarification of an error in calculated capture rates (CR) (Table 3, Kushlan 1978) is needed. Based on the measured success rates (P) and HT used above, $CR_{\text{rob}} = 0.52 \text{ prey/min}$, $CR_{\text{stand}} = 7.07 \text{ prey/min}$. (The complete comparative data base then becomes: for robbing $P = 0.27$, $E_{\text{prey}} = 9.2 \text{ kJ}$, $CR = 0.52 \text{ prey/min}$, $E_{\text{gross}} = 4.8 \text{ kJ/min}$, $HT = 0.517 \text{ min}$, $E_{\text{cost}} = 3.51 \text{ kJ/min}$; for standing $P = 0.58$, $E_{\text{prey}} = 7.11 \text{ kJ}$, $CR = 7.07 \text{ prey/min}$, $E_{\text{gross}} = 50.3 \text{ kJ/min}$, $HT = 0.082 \text{ min}$, $E_{\text{cost}} = 0.351 \text{ kJ/min}$.) Based on field data, CR for a searching/standing egret is 0.26 prey/min . Thus for a robbing incident, a bird obtains $(E_{\text{gross}})(HT_{\text{rob}}) = (4.8 \text{ kJ/min})(0.517 \text{ min}) = 2.48 \text{ kJ}$. For continuing to search and capture by standing, a bird

obtains $(E_{\text{prey}})(CR_{\text{search}})(HT_{\text{rob}}) = (7.11 \text{ kJ/prey})(0.26 \text{ prey/min})(0.517 \text{ min}) = 0.956 \text{ kJ}$. The net energy for robbing is $2.48 \text{ kJ} - (E_{\text{cost}})(HT_{\text{rob}}) = 2.48 \text{ kJ} - (3.51 \text{ kJ/min})(0.517 \text{ min}) = 2.48 \text{ kJ} - 1.81 \text{ kJ} = 0.66 \text{ kJ}$. The net energy for searching and standing is $0.956 \text{ kJ} - (E_{\text{cost}})(HT_{\text{rob}}) = 0.956 \text{ kJ} - (0.351 \text{ kJ/min})(0.517 \text{ min}) = 0.956 \text{ kJ} - 0.181 \text{ kJ} = 0.77 \text{ kJ}$. The equivalent cost/benefit comparison is: robbing $c/b = 1.81/2.48 = 0.73$; standing $c/b = 0.181/0.956 = 0.19$. Based on either maximizing net energy gain or minimizing cost/benefit ratio, robbing should not be preferred to continued standing.

By each of these net energy and cost/benefit analyses, using either efficiency or net energy as criteria, robbing should not be added to a standing repertoire. Suggesting that a mixed behavioral strategy may not be maximizing a feeding function in a specific situation should in no way undermine the heuristic value of the theoretical approach to feeding ecology. To the contrary, as I have indicated (Kushlan 1978) and as was convincingly discussed by Pyke et al. (1977), this approach has met with encouraging successes in predicting solutions to maximizing foraging and, even more importantly, has allowed the posing of decisive questions derived from a new perspective. Some of these questions might be: do animals alter foraging effectiveness between rigorous and nonrigorous conditions, or is achieving energy adequacy rather than maximization sometimes permissible? The possible ramifications of positive answers may make such questions well worth examining.

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