

ENERGY MAXIMIZERS AND TIME MINIMIZERS: THEORY AND REALITY

By relating the time and energy involved in foraging to potential fitness, Schoener (1969, 1971) introduced the concepts of "time minimization" and "energy maximization." The basis of his original distinction is the extent to which food-energy input during a given time period contributes to an animal's ultimate reproductive success. For a feeding-time minimizer, input beyond a certain net energy gain does not increase potential reproductive success. Such animals may thus minimize their foraging periods and so allow time for other activities. Schoener (1971) generally considered animals with relatively fixed reproductive outputs, and males more often than females, as being time minimizers. A food-energy maximizer, on the other hand, is an animal whose potential reproductive success is an increasing function of its net energy gain. Schoener (1971) generally considered animals with variable clutch sizes, and thus females rather than males, as being energy maximizers.

These concepts are of more than heuristic value; they intrinsically predict that these forager types will behave differently in any given environment. Indeed, recent theoretical explorations have generated experimentally falsifiable predictions that these foragers will respond in opposite directions to certain environmental variations (e.g., Hixon 1980). Before such predictions can be tested rigorously, however, one must be able to classify the animal in question both independently and unambiguously as being either a time minimizer or an energy maximizer. Thus, these concepts not only must be more explicitly clarified on a theoretical level, but also developed on a practical level by some clearly definable empirical criterion. This is my purpose here. However, I conclude that there are presently insufficient data to so classify most animals.

Although intuitively appealing, the original formulation of the time minimizer-energy maximizer dichotomy contains certain ambiguities. First, assigning a predominant sex to either forager type may not be justifiable. For example, sexual selection may result in young growing males maximizing their energy input toward the earliest possible attainment of size-dependent social dominance (see Trivers 1972). Similarly, where large-size classes are relatively invulnerable to predation, selection may favor small individuals of either sex being energy maximizers. Finally, both sexes may act as energy maximizers to some extent when excess food energy can be stored physiologically for later use (see Pianka 1976).

Second, and more important, selection is likely to favor any animal maximizing its net energy input in a minimum amount of time while actually foraging (Pyke et al. 1977). Thus, the only real distinction between these forager types may be that, during a given time period available for foraging (and I stress available), a time minimizer stops foraging after obtaining some net energy requirement, while an energy maximizer continues to forage throughout the entire period. In essence, the relative proportion of available time spent foraging becomes the sole distin-

guishing criterion (see Hixon 1980). In this sense, any animal during any given time period becomes strictly one or the other type of forager. (Perhaps these foragers should be renamed simply "feeding-time minimizers" and "feeding-time maximizers.") Note that, given the empirical basis of this criterion, an energy maximizer in Schoener's original sense that became satiated and stopped foraging during the period in question could be labeled a time minimizer (Hixon 1980). Similarly, an otherwise time minimizer that did not fulfill its net energy requirement and thus foraged continuously during the same period would be labeled an energy maximizer. Obviously, the given time period becomes an important factor (see Katz 1974). In this discussion, I consider an average daylight period for diurnal animals.

On a relative scale, this distinguishing criterion may be empirically useful for comparisons within a given species occupying a particular habitat, thus controlling for most environmental influences. For example, although the sexes are monomorphic and consume the same prey, females within the temperate reef-fish genus *Embiotoca* spend much more time foraging than males (Hixon 1979), and thus may be considered energy maximizers relative to males.

On an absolute scale, however, this empirical criterion creates a new problem: How does an observer determine what time is "available" for foraging? In the case of animals that forage virtually constantly, such as goldcrests (*Regulus regulus*) during mid-winter (Gibb 1954, 1960), the label of energy maximizer is obviously appropriate. The crux of the problem lies in classifying apparent non-foraging time. One solution would be for the observer to somehow rank the animal's activities in terms of survival and reproductive importance relative to foraging. Time spent on immediately essential activities would be considered time "unavailable" for foraging. Thus, animals that forage constantly, except when avoiding predators, defending territories, or engaging in reproductive activities, may be labeled energy maximizers. A possible example among coral-reef fishes are juvenile parrotfishes (genus *Scarus*) that appear to graze throughout the day, except when briefly sheltering in the presence of passing piscivores (personal observation; see also Ogden and Buckman 1973). On the other hand, certain top carnivores, such as lions (*Panthera leo*), spend large amounts of time simply lounging between kills (Schaller 1972), and thus can be readily labeled time minimizers.

However, classifying (let alone ranking) activities may often be difficult, if not impossible. Consider an animal that is sitting still in the absence of predators. If that animal is searching or waiting for prey, or even emptying its crop between successive feeding bouts, then sitting time is actually foraging time and the animal may be labeled an energy maximizer. If, however, that animal is scanning for the presence of predators or competitors, then sitting time may or may not be considered time available for foraging. Moreover, how is an observer in the field to know which of these or other alternatives motivates sitting at any given time? The immediate problem is obvious and the original problem remains.

Thus, simple time-budget data alone often cannot effectively distinguish time minimizers from energy maximizers. Such classification requires thorough behavioral and physiological field analyses of both the time and energy budgets of

the animal in question. Unfortunately, these data are lacking for a vast majority of species. Perhaps the best known animals in this regard are hummingbirds, and even in this case an unequivocal label is presently impossible. These small, often territorial nectar feeders exhibit virtually fixed clutch sizes (Welty 1975), must at least balance their energy budgets daily (Calder and Booser 1973; Carpenter 1974), individually tend to forage over a constant number of flowers on successive days (e.g., Gass et al. 1976; Lyon 1976; Kodric-Brown and Brown 1978; Gass 1978; Hixon et al. MS), usually spend about 75% of the day sitting in the apparent absence of predators (e.g., Stiles 1971; Wolf and Hainsworth 1971; Ewald and Carpenter 1978; Hixon et al. MS), and have been classified previously and reasonably as time minimizers (Wolf et al. 1975; Hixon 1980). However, recent field measurements have shown that migrant individuals of at least one species (*Selasphorus rufus*) may progressively gain weight each day (F. L. Carpenter and D. C. Paton, unpubl. data), and optimal meal-size considerations (DeBenedictis et al. 1978) suggest the possibility that sitting bouts may actually constitute crop-emptying time between successive feeding bouts. These data support the idea that such birds may in fact be energy maximizers, with sitting time representing necessary "handling" time while foraging. Ongoing research should more precisely clarify this dichotomy for hummingbirds. One can imagine the difficulty of classifying less intensely studied animals.

Should we, then, abandon the time minimizer-energy maximizer dichotomy on an empirical level? I think not, but I hope that this dialectical discussion has underscored the idea that these labels can be assigned with confidence only after thorough field analyses of time and energy budgets, analyses which are presently lacking for most species. The fact remains that these different forager types do exist and that they can be expected to respond differently to certain environmental variations, as has been shown theoretically for factors determining feeding-territory size (Dill 1978; Ebersole 1980; Hixon 1980). Unfortunately, until the necessary baseline analyses are made, the predictions of such models will remain experimentally testable but untested.

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