

designed to provide predictions of the foraging behavior of individuals, assuming that natural selection acts on the individual and that an individual can maximize its reproductive fitness by optimizing its foraging behavior. Gaines tested many of her hypotheses with data on flocks of American Tree Sparrows; these data do not necessarily reflect decisions made by an individual.

Foraging models are useful tools which provide testable hypotheses to compare with an organism's foraging behavior. Several good examples of field tests of optimal foraging theory have shown that predators can optimize their foraging behaviors (e.g. Belovsky 1978; Lima 1983, 1985; see also Krebs et al. 1983, Pyke 1984 for reviews). Stephens and Krebs (1986) provide an excellent discussion on problems in testing foraging models and how to appropriately design tests of various models. Their recommendations should be considered when designing foraging studies to avoid inappropriate tests of the models, which could result in confusing evidence that actually neither supports nor contradicts optimal foraging theory.

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Response to Tome

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The primary mechanism by which science advances involves interactions among peers. Foraging theory is no exception to this, as Tome's (1989) commentary so clearly demonstrates. The focus of his comments concern an experiment I conducted (1989) to examine foraging responses among wild American Tree Sparrows (*Spizella arborea*). Tome raised valid points concerning my specific working assumptions and indicated ways in which future attempts at empiricism might circumvent ambiguous results. One was through careful consideration of assumptions associated with foraging hypotheses. Since I conducted my experiment (1982/1983), Stephens and Krebs (1986) produced their monograph on foraging theory. With Ste-

phens and Krebs as a guide, Tome outlined specific areas where experimental designs can be improved.

I attempted to simultaneously assess predictions from three different models. Simple, first generation models were chosen intentionally so that experiments could be designed to produce mutually exclusive alternative hypotheses. Trials were conducted during the winter to avoid complications of reproductive behavior. At this time of year, Black-capped Chickadees (*Parus atricapillus*) were also common in grasslands. I selected seed large enough to exclude them from foraging on the experimental grid. Rodents were trapped and removed from the area. Except for one Harris' Sparrow (*Zonotrichia querula*) observed for two days during a blizzard, no other seedeaters were ever observed on the grid, and I felt completely confident that the seeds removed from the grid were taken exclusively by Tree Sparrows. Flock sizes remained relatively constant (9-13 individuals) throughout the

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experiment so that the mass of seed applied before each trial was designed to accommodate the flock during the 24 h trials.

Tome's concern about flocks, as opposed to individuals, that visited the patches is valid and was pondered a priori. I chose to follow the most realistic pathway and allowed the birds to forage in their typical fashion during the winter (as flocks). Before the experiment, >100 observer hours were logged to determine if individual interactions among members of the flock had any effect on the location or duration of foraging in patches. Additionally, >200 h of observations during experimental trials were subsequently excluded because snow fell or blew in the grid and covered the seed. Individuals arriving at the grid entered occupied and vacant patches with equal frequencies (627 and 593, respectively) so that flock dynamics did not appear to affect patch selection by individuals.

What Tome failed to note is that there could have been a certain amount of empirical bias imposed by flocks, which applies specifically to the predictions I used to test the MVT. The mass of seed removed from low-quality patches was higher than expected. This could be due either to a few individuals with long residence times or several individuals with short residence times. In either case, further analyses of predictions and tests of the MVT which specifically address this point are needed to determine the manner in which individuals function in group foraging situations.

The problem of revisitation is an important one. Tome points out that once a patch has been exploited, according to the models, it should not be revisited. My experimental design intentionally violated this assumption, but in doing so I tried to minimize the impact of revisitation. Tome states that the large amount of variation between patches is inappropriate for examinations of time or gain expectation models. My experimental design required large amounts of variation between patch types so that highest quality patches remained high *even if revisitation occurred*. Additionally, the MVT examines residence time, not patch selection. The amount of variation between patches should not significantly affect model predictions. Finally, I still feel that the prediction of the marginal value model (patches should be reduced to the same marginal gain rate) was not supported. Seed reductions in lowest quality patches were too great too consistently to be attributed to anything but active foraging by tree sparrows.

Tome claims that the MVT formula contains sepa-

rate parameters which account for energy costs of traveling between and searching within patches. The version of the MVT model which I chose to use (1989: 120, fig. 1) equates these two terms and so generates an internal (mathematical) assumption that costs are equal. Given the proximity of patches, this is also sound biologically. This assumption, without any information on physiological costs, would not have affected significantly the results, whereas inclusion of parameter estimates without empirical basis would likely have produced even more "ambiguous" results.

Tome failed to analyze a critical MVT assumption: that the gain curve is smooth, continuous, and decelerating. More and more, researchers report that the gain curve may take different shapes. During residence time within a patch, individuals tend to show more linear gain curves, with departure occurring before deceleration of gain rates (Stephens pers. comm.). Gain curves in this experiment probably also tended toward linearity, given the large amounts of seed available during a trial. The effect this assumption has on MVT predictions is extremely important and can only be assessed through careful behavioral observations.

Tome and I agree that my data do not constitute robust falsification of the MVT. They do show that tests in natural systems require that models are refined using specific sets of constraining functions. More complete information concerning behavioral variation among individuals is key to analyses of group foraging situations. The failure of MVT to be supported in this case strongly suggests that group dynamics and individual behavioral variation are factors which must be included in constraining functions, not that the model is wrong.

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