Comparisons of Patch-use Models for Wintering American Tree Sparrows

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Optimal foraging theory has stimulated numerous theoretical and empirical studies of foraging behavior for >20 years. These models provide a valuable tool for studying the foraging behavior of an organism. As with any other tool, the models are most effective when properly used. For example, to obtain a robust test of a foraging model, Stephens and Krebs (1986) recommend experimental designs in which four questions are answered in the affirmative. First, do the foragers play the same "game" as the model? Second, are the assumptions of the model met? Third, does the test rule out alternative possibilities? Finally, are the appropriate variables measured? Negative answers to any of these questions could invalidate the model and lead to confusion over the usefulness of foraging theory in conducting ecological studies.

Gaines (1989) attempted to determine whether American Tree Sparrows (*Spizella arborea*) foraged by a time (Krebs 1973) or number expectation rule (Gibb 1962), or in a manner consistent with the predictions of Charnov's (1976) marginal value theorem (MVT). Gaines (1989: 118) noted appropriately that field tests of foraging models frequently involve uncontrollable circumstances; thus, it is often difficult to meet the assumptions of the models. Gaines also states (1989: 118) that "violations of the assumptions are also informative but do not constitute robust tests of predicted hypotheses," and that "the problem can be avoided by experimental analyses which concurrently test mutually exclusive hypotheses so that alternative predictions will be eliminated if falsified." There is a problem with this approach because, when major assumptions of models are not satisfied, it is not justifiable to compare a predator's foraging behavior with the model's predictions. I submit that failing to follow the advice offered by Stephens and Krebs (1986) can invalidate tests of foraging models.

Gaines (1989) summarized several important assumptions of the MVT, but overlooked the assumption that patches are numerous enough so that they are not revisited by the predator. Gaines observed a foraging arena that contained only 5 food patches. An observer was present for a small fraction (50 h) of the twenty-four 24-h trial periods when the patches were exposed to any seedeating species. It was impossible to determine how many times during a trial the unbanded American Tree Sparrows or any other avian seedeater visited or revisited the foraging arena. If the American Tree Sparrows revisited the patches, a major assumption of the MVT was violated;

likewise, if other avian seedeaters foraged in the patches, the results would be confounded further.

Gaines used the number of seeds that remained in patches after 24 h to determine if American Tree Sparrows maximized their net rate of energy intake. Rigorous testing of the MVT depends upon obtaining an estimate of the instantaneous rate of energy return at the moment the patch is abandoned (Charnov 1976). Simply measuring the seed mass remaining after 24 h does not provide this information, particularly when a flock of birds is exploiting the habitat. The rate of net energy intake at any given time may depend upon the number of competitors in a flock, the distribution of seeds in the patch, or time engaged in other activity (i.e. predator avoidance).

Assumptions of the time and number expectation models also appear to have been violated. These models also are valid only when a predator does not revisit exploited patches. If the predator follows a number expectation rule, it should consume the "appropriate" number of prey, abandon the patch, and not return to that patch because the patch is no longer profitable, unless the food is replenished before the patch is revisited. In addition, Krebs et al. (1974) note that the number expectation rule is only appropriate if all patches contain similar numbers of prey. The patches in Gaines' experiments contained between 50 and 250 g of sunflower seed; this variation is probably too extreme to assume that predators should employ a time or number expectation rule.

Gaines (1989: 120) incorrectly states that the MVT requires that travel time between patches and foraging time within patches must have equal energetic costs. In fact, the MVT formula (Charnov 1976: 131) contains two parameters that account for each of these: E_T, the energetic cost of traveling between patches, and E_{si}, the energetic cost of searching within a patch.

Gaines also incorrectly states that the MVT predicts that high-quality patches be selected more frequently than low-quality patches until all patches are reduced to the same rate of return. The MVT does predict that all patches will be reduced to the same marginal rate of return (Charnov 1976), but it does not predict that good patches will be selected more frequently than patches of lower quality. In fact, the predators should stay in each patch, as it is encountered, until the marginal rate of return from that patch equals the average rate of return for the habitat (Charnov 1976: 132). Once a patch is abandoned, it should not be revisited (see above). Thus, a predator may exploit a high-quality patch longer than a low-quality patch (depending on the relation between energy gain and time spent in the patch), but high-quality patches should not be *selected* preferentially over lower quality patches.

Finally, the MVT and the expectation rules were

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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.

I thank R. Michael Erwin and Gary E. Belovsky for reviewing a draft of this Commentary.

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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 Stephens 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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