

COMPARISONS OF PATCH-USE MODELS FOR WINTERING AMERICAN TREE SPARROWS

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ABSTRACT.—I investigated three mutually exclusive patch-use hypotheses for wintering American Tree Sparrow (*Spizella arborea*) flocks. An experimental design with five ranked patch types that differed by the mass of supplemental sunflower seed added to each was employed. Daily repetitions were grouped into three "environments," with harshness rankings based on the presence of snow cover and average daily temperatures. Tree sparrows spent equivalent times in all patch types but, because search plus handling times for patches differed, the birds removed different total amounts of seeds. Two models measured the amount of seed removed from each patch and were falsified. Neither the rate of seed consumption nor the total mass consumed were equivalent among patches. Tests of a third model supported the hypothesis that equivalent periods of time were spent in each patch. Foraging patterns did not follow predicted rankings of environmental harshness for temperature, as low seed visibility during repetitions without snow cover greatly reduced total amounts of seeds eaten. Received 14 March 1988, accepted 12 September 1988.

ONE aspect of foraging theory involves patch-use models (Emlen 1966, MacArthur and Pianka 1966) to help explain competition and niche separation among animals. Foraging theory posits that selection acts to maximize energy intake based on the decision-making abilities of an individual while foraging. Each of the four categories of foraging behavior models (prey choice, patch choice, allocation of time to patches, and foraging patterns) requires that individuals make a choice as to how they will forage (Pyke et al. 1977). The efficiency of these decisions can be measured empirically.

Foraging models are tested with data from field and laboratory observations to assess applicability of predictions once initial assumptions are satisfied. Violations of assumptions are also informative but do not constitute robust tests of predicted hypotheses. Tests are often designed to corroborate null hypotheses and establish models which describe behavior. Clutton-Brock and Harvey (1984) pointed out that repeated revisions of such models might be used to support one which was inaccurate but supported by descriptive data. The problem can be avoided by experimental analyses which concurrently test mutually exclusive hypotheses so that alternative predictions will be eliminated if falsified.

In the original patch-use models (Gibb 1962), an animal was expected to remain in a patch until a certain number of prey are found. The animal will leave a patch if and only if it has

secured the constant number of prey. Another model (Krebs et al. 1974) is similar but utilizes a constant time allocation for all patches. Both models assume that there are no criteria to distinguish patches and that foraging behavior is consistent from one patch to another, regardless of the patch quality. Both of these are "high risk" strategies in variable environments because they predict that an animal will use all patches equivalently (Zach and Falls 1976, Stephens and Krebs 1986).

Many of the experiments conducted to describe the allocation of time to patches of differing quality within a habitat (Cowie 1977; Pyke 1978, Bond 1980, 1981; Hodges 1981) have provided qualitative or quantitative support for the marginal value theorem (Charnov 1976). This model predicts that an individual will maximize its net energy gain while foraging in a patchy habitat if it leaves a particular patch when its net energy gain decreases to the mean energy gain level for the entire habitat.

I observed the patterns of animals leaving patches through the use of different patch types by American Tree Sparrows (*Spizella arborea*) under field conditions. The experiment was conducted during the winter and avoids many problems of individual activity patterns associated with reproduction, such as territoriality. These complicate models of foraging behavior. Certain levels of inference will be lost because of uncontrolled variation inherent in field experiments but a carefully planned experimental

design has eliminated several of these problems. Finally, winter conditions in Nebraska may magnify foraging responses because of the added costs imposed by freezing temperatures, strong winds and sub-zero wind chill indices, and a decreasing resource pool.

MATERIALS AND METHODS

Experiments were performed at the Reller Natural History Area, located south of Lincoln, Nebraska, ca. 3 km from the village of Sprague. A controlled burning regime and planting of native species has helped to reestablish portions of the area as tall grass prairie. Indian grass (*Sorghastrum nutans*) and big bluestem (*Andropogon gerardii*) represent the dominant grass species. The experimental grid area was selected because of its proximity to wooded areas which provided both foraging sites and roosting areas for wintering birds.

The American Tree Sparrow (*Spizella arborea*) is an abundant and reliable winter resident in eastern Nebraska. Although it is not an obligate granivore, its alternative food source (arthropods) is not readily available during winter in Nebraska.

Site preparation.—A 28-patch grid was developed in which square patches (5 × 5 m) were established with boundaries on each edge. Each patch was clipped, so that all remaining rooted vegetation was less than 7 cm in height, and then raked to remove excess debris. After these manipulations the patches were considered to be homogeneous with respect to the height and density of vegetation. Excess debris was piled between patches to produce distinct and consistent patch separations.

To reduce the impact of rodent foraging on the grid, I set small mammal traps in a 100 × 100 m area which completely included the grid. I trapped for eight consecutive nights before the study and all captured rodents were removed. One trap per patch was set each week during the study to maintain rodent populations at low levels.

Pre-experimental seeding was practiced during preparation stages of the experiment. Constant densities (mass/area) of seeds were spread in randomly selected patches within the grid to provide a known food source for local winter residents and to determine appropriate treatment levels to prevent food depletion. Uneaten seed was collected each day with a D-Vac insect vacuum and new patches were again randomly selected for additional trials. After 18 days of repetitions, unbanded tree sparrows were quickly able to locate patches with seeds after entering the grid area from the roosting site (patch location time = 78 s; SD = 54). During these and the experimental trials, flock sizes remained relatively constant (9–13 birds).

Other preparatory activities included patch main-

tenance for the removal of vegetation which blew or fell into the cleared patches. With each new snowfall, patches required preparation before running another repetition of the experiment. Snow was packed down on all patches to form a smooth, even crust. This was especially beneficial during windy weather when blowing snow posed potential problems to the conduct of a trial.

The experiment was conducted between 10 December 1983 and 30 March 1984. During this time snowfall often covered patches so that these trials were terminated and the data ignored. Successful daily trials were grouped into three ranked categories of environmental conditions encountered during the study. Ranks were determined based on qualitative estimates of metabolic costs (Grubb 1978) and the substrate color and visibility of the black sunflower seeds. Environment I ("O.K.") had average daily temperatures above -7°C and complete snow cover. Environment II ("Bad") was characterized by average daily temperatures below -7°C and complete snow cover. Environment III ("Terrible") had daily temperatures below -7°C and no snow cover. This organization of data allowed a two-way analysis of variance for a randomized complete block design (Cochran and Cox 1957). Repetitions were conducted until eight successful experimental trials could be included in each environment.

A small black variety of commercial sunflower seed was chosen to reduce variation in food choice. I applied lots of 250, 200, 150, 100, and 50 g, scattered throughout the assigned treatment patches. Treatments were allocated randomly to 5 patches which received a different random allocation of treatments on each of the 8 days of trials within an environmental category. The use of the same experimental units for different repetitions was justified through satisfaction of the assumption that their covariances remain the same for all repetitions. In this way travel times between patches were controlled for each repetition and predicted optimal residence times remained constant.

The area of the entire experimental grid represented a habitat with 5 patches of differing foraging qualities. Seed treatments were applied between 1200 and 1500, and remaining seeds were collected 24 h later. I weighed the residual seeds collected by vacuum.

Fifty hours of observations were made during twenty-four successful experimental trials. I determined interpatch travel time, search and handling time per seed, patch residence time, directions of movement onto and off the grid, and total number of tree sparrows that foraged in the area. Interpatch travel time was the amount of time each bird spent between patches while still on the grid and was measured from the time a bird left a patch until it picked up a seed in a different patch. Search and handling time was the total time required to locate and con-

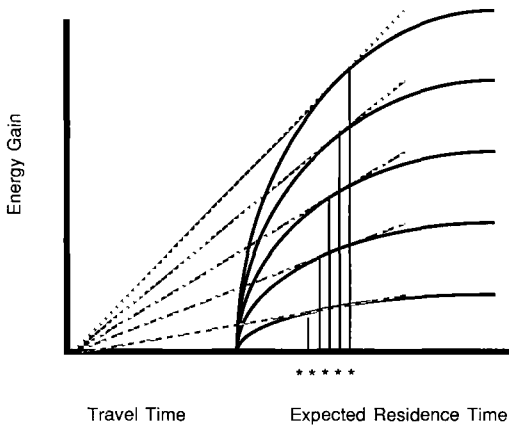


Fig. 1. The marginal value model. Expected residence times (stars) were calculated at the asymptote of the net energy gain curve for each patch type from the point when travel was initiated (stippled lines). Gain curves (solid lines) can begin only after travel time when an individual enters a patch and begins to feed. After Charnov (1976).

sume one seed and was measured from the time an individual finished consuming one seed until it picked up and consumed another seed in the same patch. Residence time for each patch was initiated when the first seed was picked up and terminated when the bird flew out of that patch and did not return. I recorded the total number and locations of all tree sparrows in the area every 20 min during each trial.

Any interruption of feeding to collect and distribute seeds was followed by an uncounted 30 min "settling period."

The models.—The expected gain model (Gibb 1962) assumes that distinct patches occur which differ in their quality and that there is no patch recognition or differentiation. The model predicts that the total mass of seeds removed is equivalent for all patches. This leads to a null hypothesis,

$$H_0: G_1 = G_2 = G_3 = G_4 = G_5,$$

where G_i = mean mass consumed per 24 h in patch i . The test compares responses by the entire foraging flock during each 24 h experimental trial. The assumptions of the expected time model are the same as those for the expected gain model, but the prediction is different. In the expected time model it is the time individuals spend in each patch type which is predicted to be equivalent (Krebs et al. 1974). This model allows the hypothesis,

$$H_0: t_1 = t_2 = t_3 = t_4 = t_5,$$

where t_i = mean observed patch residence time in patch i . This test provides a mean comparison procedure for field observations of patch residence times for individual birds as they use the grid during for-

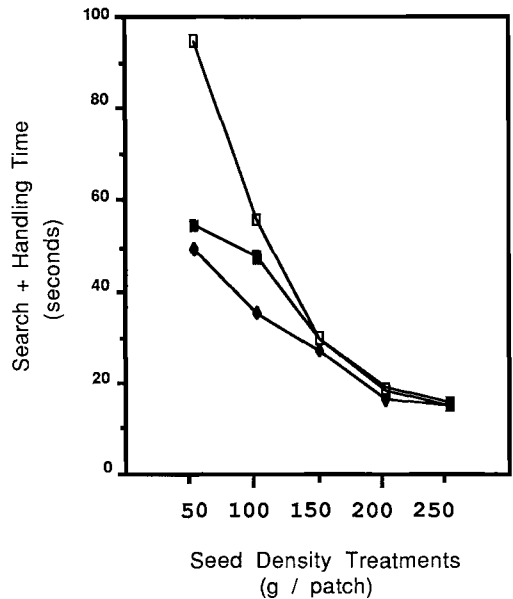


Fig. 2. Search + handling times for each of 5 patch types in 3 types of environments. Filled diamond = "O.K."; filled square = "Bad"; empty square = "Terrible."

aging. The marginal value model (Krebs and Mc Cleery 1984) assumes that each patch type is recognized instantaneously; that the travel time between patches is known by the birds; that the gain curve is smooth, continuous and decelerating; and that travel time between, and searching time within, a patch have equal energy costs. The model predicts that the optimal residence time in each patch type is a function of travel time and the gain curve. If there is more than one patch type in an environment, then all should be reduced to the same marginal gain rate. Finally, when the gain curve is known for each patch type, the predicted and observed residence times should be equal (Fig. 1).

The closeness of fit of the predicted value for all patches in the experimental environment to the observed values for each patch type were used to test the marginal gain model. I calculated estimates for marginal gain rates based on the mean residual mass of seeds left in all patches averaged over 8 days of trials in each environment category. Observed values were calculated as the average residual seed mass left in each patch type over 8 days of experiments. Comparisons were made across all environment categories as well.

RESULTS

Several assumptions of the models were met satisfactorily through the design of the experiment. Seed density treatments influenced

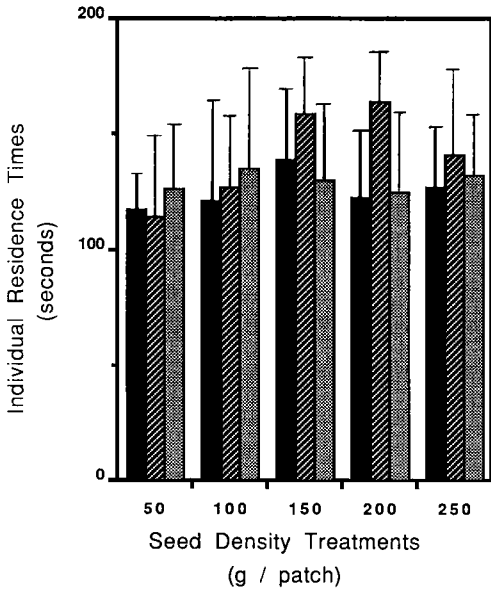


Fig. 3. Observed patch-residence times for individuals in 3 types of environments. Filled bar = "O.K."; lined bar = "Bad"; speckled bar = "Terrible." Standard errors are shown.

search and handling time within patches (Fig. 2). The nearly linear increase in rates of food intake were closely associated with the evenly spaced treatments ($R^2 = 0.93$) and implies that the series of distinct patches available within the grid represented areas of different quality. Additionally, the gain curve decelerated as the availability of food decreased, although its exact shape was unknown.

Only the expected time hypothesis was supported by the data; individuals spent similar residence times in different quality patches ($F = 1.68, P > F = .247$) regardless of varying environmental conditions ($F = 2.44, P > F = .149$) (Fig. 3). However, error values associated with the means used in the comparisons represent up to 40% of the sample means. This may suggest that differences in residence times may have been swamped by variation among individual residence times within patches.

Both the expected gain and marginal value hypotheses had significant differences among treatments ($F = 9.58, P > F = .008; F = 25.57, P > F < .001$, respectively) and between environments ($F = 9.27, P > F = .004; F = 9.01, P > F = .009$, respectively) but no interactions (Figs. 4, 5). In each case, treatment response means within environments had ranking patterns similar to the original treatment rankings.

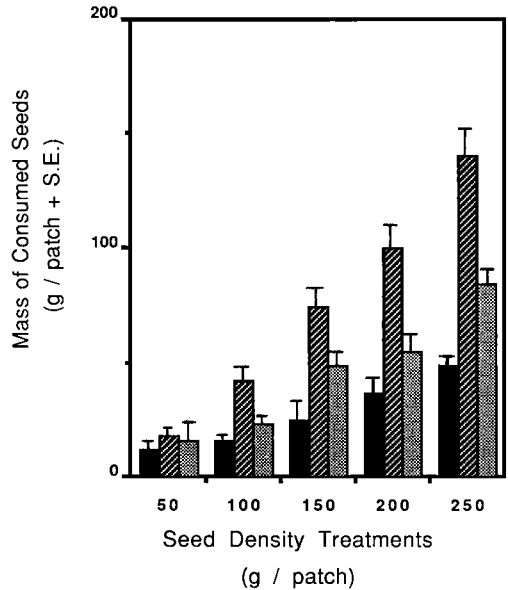


Fig. 4. Mass of seeds eaten by all American Tree Sparrows during the 24-h trials. Symbols as in Fig. 3.

Alternatively, environmental responses did not replicate a priori rankings based on temperature and visibility of seeds. As environmental conditions became more harsh (lower

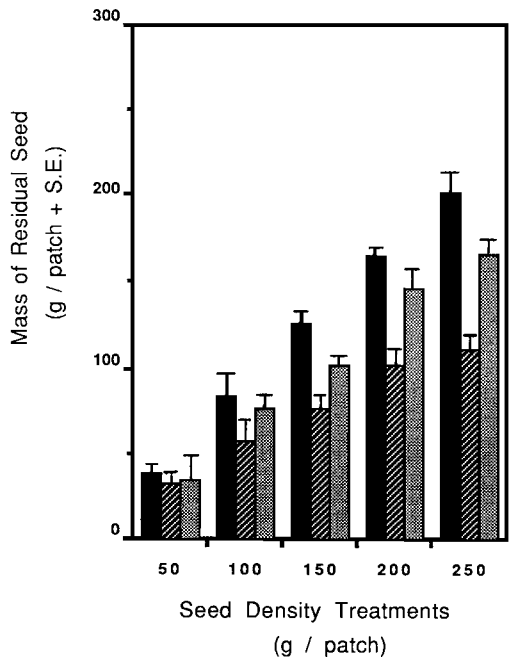


Fig. 5. Mass of residual seeds collected from patches after trials were successfully completed. Symbols as in Fig. 3.

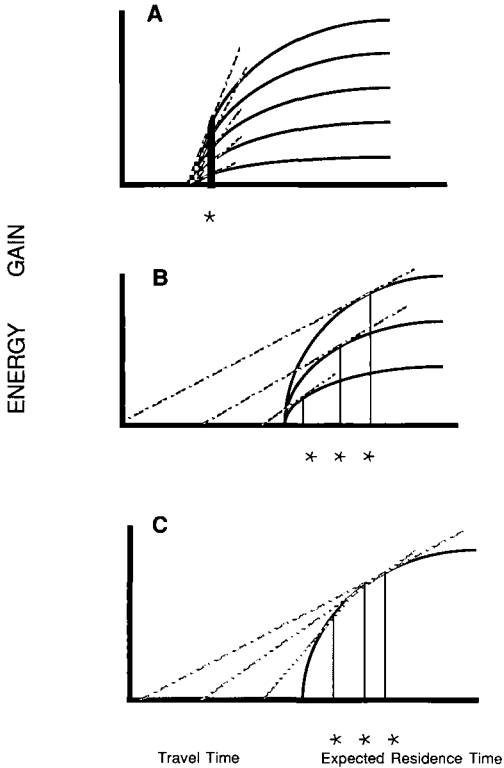


Fig. 6. Three variations of experimental designs for the marginal value hypothesis. Axes are labeled as in Fig. 1. (A) Distinct patch types produce distinct gain curves but short travel times lead to indistinguishable residence times. (B) Three distinct patch types and three distinct travel times lead to distinguishable residence times. Note that longer travel times must be associated with higher gain curves or residence times become indistinguishable. (C) All patches produce similar gain curves but travel times differ. This is the best design for exclusive testing of the marginal value hypothesis but does not allow simultaneous tests of the other models examined in this study.

temperatures), feeding rates initially increased; but under the harshest conditions (low visibility of seeds and low temperatures), feeding rates decreased. Increased food intake was expected as environmental conditions deteriorated and the seed mass consumed by flock members during trials nearly doubled as temperatures dropped below -7°C .

DISCUSSION

Field tests of foraging models include higher levels of experimental error than do most lab-

oratory tests. This requires certain considerations in the planning and design of experiments. The expected time and expected gain models were tested rigorously with respect to their assumptions and predictions. Because treatment densities produced different foraging rates (Fig. 2), tests of these models were mutually exclusive; either or both could be falsified, but both were not supported simultaneously.

Support of the expected time model suggests that, for American Tree Sparrows foraging under adverse conditions (Grubb 1978), time away from protected roosting sites is a critical factor. The number of food items secured in each patch was not constant, which suggests that at least some patch recognition or distinction may have occurred.

If there are patches that differ in quality, the marginal value theorem states that all patches should be reduced to the same marginal gain rate for the entire habitat. In this situation, high-quality patches should be selected much more frequently than low-quality patches until the high-quality and low-quality patches produce the same gain rate. Only then would patches be exploited to the same level. A test of the hypothesis showed that this was not the case and that low-quality patches were used for similar amounts of time as high-quality patches well before the gain rate for higher-quality patches dropped to that for low-quality patches. The only prediction I examined was that all patches should be reduced to the same marginal gain rate; it may be questioned whether it provided a rigorous test of the marginal value hypothesis. Falsification of any of the predictions demonstrates a lack of support for a model. Examining all predictions requires satisfying all assumptions. This cannot be accomplished simultaneously for this model in part for reasons discussed below.

Different experimental designs may inadvertently fail to adequately address the model (Fig. 6). Expected residence time was a function of travel time to a patch, and patches must be widely separated if an effect of patch differences is the objective of investigations (Fig. 1). In my experiment, patch qualities differed but the distance between them was so small that I could not distinguish between residence times for each patch type when the magnitude of variation was included in predicted residence times (Fig. 6A). More robust tests of the marginal value

theorem must incorporate both patch differences and increased travel times (Fig. 6B) or just different travel times (Fig. 6C). Logistical problems may arise with field tests in which travel times alone are great enough to produce significant effects. In some cases travel times must be two- or threefold greater than residence times. This may confound results if a majority of foraging occurs outside the study area. As an alternative, these results show that the shape of the gain curve and differences between patches can be manipulated in experimental designs to minimize distances between patches relative to residence times.

Although initially planned as a set of three mutually exclusive hypotheses and tested so that only one hypothesis could be supported at any one time, high levels of variation in foraging responses by individuals and flocks may have compromised the rigor of tests of the expected time hypothesis which failed to be falsified. Gain rates were successfully manipulated for wild birds which indicates the applicability of field studies for foraging hypotheses. Understanding the way birds exploit patchily distributed food in the natural environment is essential to foraging theory, and this study has demonstrated one way that such studies can be conducted.

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