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Predicting the distribution of organisms among a few patches: problems with detecting departures from the ideal free distribution

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Much empirical work has examined whether foraging animals distribute themselves across patches of resources according to an ideal free distribution (IFD). Most studies consider situations with 2 patches, where choice of one patch is synonymous with rejection of the alternative. In this paper, we use computer simulations to determine the effect of the number of patches on achievement of an IFD. Identical foragers were allowed to move between patches so as to maximize their intake rate. To generate departures from an IFD, we assigned all foragers a perception limit of prey numbers such that they could not perceive differences in patch quality that exceed this limit. Foragers would choose randomly from the patches among which they could perceive no differences. We found that, for the same perception limit, departures from an IFD were greatest in the 2-patch situation. In addition, we are less likely to detect perception limit-generated deviations from an IFD (or even a random distribution) in greater than 2-patch situations unless we examine cases in which there are large among-patch differences in quality. Hence, lab and field studies that incorporate the greater realism achieved by using more than 2 patches must be cautious about falsely accepting the hypothesis of an IFD, particularly if the causes of deviations from an IFD are independent of the number of patches. We review published studies and find that conformity to an IFD seems to decrease with an increase in the number of patches. Hence, if deviations from an IFD are perception-induced, discrimination may decrease with the number of patches, presumably because of the increasing physical and computational difficulties of keeping track of each patch.

The ideal free distribution (IFD) of Fretwell and Lucas (1970) forms the theoretical spine of dozens of studies that consider how organisms competing for limited resources should distribute themselves between alternative patches of these resources. When resources are replenished at a continuous rate, and are consumed immediately, the IFD predicts that all organisms should achieve equal rates of resource acquisition whenever competitors are identical, possess a perfect knowledge of their environment, and can move freely among patches. As a consequence of IFD conditions, the relative number of organisms in a patch should match the relative resource availability in that patch, when the functional response is linear and handling times are negligible. Despite the restrictive assumptions of equal competitors, omniscient decision-makers, and free access to resource patches, a remarkable number of studies, usually performed on foraging animals in controlled laboratory conditions, have found qualitative support for IFDs (Milinski and Parker 1991).

In most of the experimental studies testing IFDs of the continuous input type (as described in the previous paragraph), foragers choose between only two patches. The two-patch case is presumably favoured for its experimental simplicity. However, the two-patch system represents a special case, because a forager’s choice of one patch directly lowers the proportion of individuals in the other, leading to a situation of non-independence. In situations with more than two patches, an organism rejecting one patch still has a choice of two or more others, such that the proportion of non-independent choices decreases with number of patches. Two-patch, or few-patch, situations may therefore possess unique attributes that can have important consequences for studies of patch choice behaviour, such that extrapolating to multi-patch systems may even be problematic.

In this paper, we consider the consequences of varying the number of patches on the likelihood of detecting significant departures from the IFD (and from a random distribution). We use computer simulations to illustrate how a violation of one IFD assumption – namely that organisms have perfect knowledge of their environment – can be detected in the distribution of organisms among numbers of patches. We review pub-
lished studies to examine how the number of patches affects the distribution of foragers. We finish with a number of methodological suggestions that aim to strengthen the ability of further experimental tests to statistically detect departures from IFDs.

**Simulations**

A common observation in tests of IFDs is that good patches (i.e., those whose resources are greater than the environmental mean) are under-used and poor patches overused, leading to “under-matching” (Kennedy and Gray 1993). One mechanism that will produce such a departure from an IFD (and there are others, e.g., Sutherland and Parker 1985) is a limit in the ability of organisms to detect differences in quality between patches (Abrahams 1986). When differences in profitability between patches cannot be perceived, organisms might select among such indistinguishable patches randomly. It is this imperfect perception mechanism that we now use to explore how differences in number of patches affects the realized distribution of organisms. In particular, we focus on the slope of the regression of percent food in a patch on percent foragers in a patch. For an IFD, this slope is unity.

We simulated the distributions of 100 identical individuals foraging for 500 identical prey items in environments that varied in the proportion of all food in an arbitrary focal patch (10 to 90%) and in the number of patches (2 to 8). For each level of food in the focal patch, the remaining food was divided equally among the other patches. We modelled perception limits in terms of the number of prey/forager that a forager could detect. The detection of profitability is assumed to be a threshold trait; any differences below the perception limit are equally indistinguishable, and differences above the perception limit are perfectly detected. In these simulations, we first distributed all foragers sequentially into the environment using the rule described in Abrahams (1986): i.e., select the currently most profitable patch (based on present levels of food and competitors in each, and including its own presence in the patch in determining profitability), or choose randomly among patches whose profitabilities are indistinguishable. The extent of indistinguishability results from the size of the perception limit; the higher the perception limit, the more likely that two or more patches will appear similar to a decision-maker. To consider the equilibrium distribution of foragers, we then perturbed the distribution of foragers by removing a single forager, chosen randomly, from its present patch. The forager then selected a patch again based on the same patch choice rule used to fill the habitat with foragers. We term this process “displacement”. This process was repeated 10 times, and the mean number of foragers in the focal patch was recorded. We assume resources are replenished at a continuous rate and are consumed immediately, with no prey handling time, and no competitive interference. A perception limit is our device for allowing foragers to make “mistakes” in their patch choices, in this case caused by the inability to detect small differences in patch quality. We do not claim that this kind of perception limits mechanism accounts for the behaviour of real foragers, although it seems biologically plausible. Instead, we use mistakes of this sort as a pedagogical device for generating departures from an IFD, so that we can then consider how the number of patches uniquely affects deviations from an IFD. However, we recognize that the particular mechanism used to generate departures from an IFD may influence the effect of the number of patches. For each level of food in a focal patch, we assumed that the remaining resources were equally distributed between the other patches. We calculated the expected distribution of foragers in the focal patch with respect to the proportion of food in the focal patch, perception limit, and number of patches, and performed 25,000 simulated trials for each combination of parameters. To calculate slopes, we performed regressions predicting proportion of foragers in the focal patch from proportion of food in that patch.

**Results**

Incorporating a non-zero level of “mistakes” causes deviations from an IFD in the direction predicted by the perception limits model (Abrahams 1986); namely over-use of poor patches and under-use of good ones (Fig. 1). Forager densities are below the IFD expectation at food levels higher than the habitat mean (i.e., higher than 100/[no. of patches]), and above the IFD expectation at food levels lower than the habitat mean. Inspection of the probability distribution of expected foragers helps explain this result (Fig. 2 shows the two-patch case). For example, if 80% of the foragers are in the good patch (with 80% of the resources), then 80% of randomly displaced individuals will be selected from this patch (since every forager has an equal probability of being displaced). If the displaced forager cannot discriminate between the profitabilities of the alternative patches, it will choose either patch with equal probability. But, as we have just described, foragers forced to make this choice are not selected from either patch with equal probability. Hence, net movement must be toward the poor patch, forcing the mean away from the extremes, such that the rich patch becomes under-used and the poor one overused. With increasing values of perception limits, the erosion of an IFD is further exacerbated because the proportion of times that displaced foragers choose patches randomly is increased. When all patches have equal numbers of foragers (because they have equal levels of food), then
Fig. 1. Changes in the relationship between percent foragers in a patch and deviations from an IFD (top row) or percent food in that patch (bottom row), for different levels of perception limit (1, 3, and 5 prey/forager) and different numbers of patches (2 to 5). The dashed line shows the expectation for an IFD (both rows). The shaded line shows the slope for a random distribution of foragers (bottom row). Numbers labelling each curve indicate perception limit. To indicate the likelihood of achieving a particular patch quality (under the assumption of randomly-determined patch qualities), the curve at the bottom of each graph shows the expected frequency distribution of patch qualities (scaled such that the Y axis also shows probability of occurrence (times 100)).

There is no disproportionate displacement of foragers from any patch, and consequently no change in the mean number of foragers with changes in perception limits (Figs 1 and 2).

The symmetry of the expected distribution of foragers, detailed in Fig. 2 for the two-patch system, is also revealing. It is skewed to the left in poor patches, symmetrical when alternative patches are of equal profitability, and skewed right in rich patches. The skew appears to result from a sharp discontinuity whereby differences in profitability among patches exceed the patch-choosing forager’s perception limits (which, recall, is a threshold trait), such that there is always a single identifiable most profitable patch. The result is a truncated normal distribution.

Mistakes (expressed here as a perception limit), then, cause an under-use of good patches and an over-use of poor ones, compared to the IFD case (Fig. 1, bottom row). The greater the level of mistakes, the greater the deviation from an IFD. However, there is also an effect of number of patches on this pattern of “under-matching”. In the two-patch situation, the different curves pass through, or “pivot” on, the 50% food level. In the three-patch situation, they pass approximately through the predicted 33% food level (which is the point at which all patches have the same amount of food), and the pivot value becomes 25% in the four-patch situation, and 20% in the five-patch situation. An important consequence of this pattern is that deviations from an IFD (using the method of relating forager to food abundance with linear regression) are equally easy to detect at low and high food levels in the two-patch situation, but are increasingly harder to detect at low food levels as the number of patches increases, even when the degree of mistake-making is relatively high. If patches in nature differ from each other according to some uniform random process, then the probability of encountering patches that differ from each other dramatically also decreases with number of patches (Fig. 1; note how the skewness of the frequency distributions of randomly determined patch qualities increases with...
number of patches). This difficulty in detecting deviations from an IFD with increasing numbers of patches holds even if slope methods, problematic for the lack of statistical independence of their points, are not used. For example, a *t*-test comparing observed and expected numbers at a single (focal) patch would still encounter reduced variation as the number of alternative patches increases, unless the focal patch is disproportionately rewarding (Fig. 1, top row).

To simplify comparisons among different conditions, we use linear regression to characterize the relationship between percent resources and percent foragers, even though the actual relationships are non-linear (Fig. 1, bottom row). When used in a comparative context, minimal distortion is introduced by treating the relationship as linear. Inspection of such regressions reveals that not only does the pattern of slope lowering change with number of patches, but so too does the magnitude of slope depression. For any non-zero level of mistakes, the slope is lowest in the two-patch case (Fig. 3). As the number of patches increases, the slope increases to an asymptote. The effect of number of patches on slope is a direct consequence of the location of the “pivot” point, which, as noted above, is the point at which all patches are of equal quality. In the two-patch situation, deviations from an IFD pull the line down at high food levels, and push it up at low food levels, with the two effects being of equal magnitude. As the number of patches increases, the major effect is to pull the line down for high food levels. Consequently, deviations from an IFD are most easily detected when patches are few.

**Discussion**

These simple, heuristic results have important implications for studies of IFDs. Clearly, for a constant number of identical foragers each with the same probability of making mistakes, and a constant amount of food, the departure from an IFD is greatest in a two-patch system. Hence the two-patch system offers the experimenter the greatest statistical power, in the sense that it can most easily detect an effect if it is really there. This represents a complication for most field studies, where the number of alternative patches often far exceeds two.

In systems with more than two alternative patches available to foragers, experiments need to focus on situations in which there are large differences among patch qualities. That is, to statistically distinguish among the lines representing different perception limits in the five-patch case (Fig. 1), we need data from cases where the food in the focal patch exceeds 40% (so that the remaining food is distributed across four patches). In multi-patch systems, we are less likely to reject the hypothesis of an IFD, even if no IFD exists (say, because of perception limits), without explicitly considering cases where patches differ greatly in food level.

Thus far, we have treated departures from an IFD, measured as differences in slope between observed and expected regression lines, as the sole trait of interest. The other side of the coin, and perhaps an equally interesting question, is whether distributions differ from random (i.e., the grey horizontal lines in Fig. 1, bottom row). As was the case for departures from an IFD, deviations from a random distribution, given some non-zero level of mistake-making, are also more difficult to detect when there are many patches and the focal patch does not have at least twice the food input level as each of the others (Fig. 1).

Houston et al. (1995) have also modelled the case of foragers who have a probability of switching among patches, at least in the case of a two-patch system. They show that the phenomenon of “under-matching” can even result in the absence of perception limits, given finite switching rates. Our results suggest that the effect of switching rate that Houston et al. (1995) model will also be less detectable as the number of patches increases, when switching can be accomplished among many alternative patches.

The majority of laboratory studies of forager distributions in conditions where resources are continuously replenished have been performed on two-patch systems, and many of these have detected significant departures from an IFD (reviewed in Kennedy and Gray 1993). Given the results of our simulations, we predict that regressions of proportion of foragers vs proportion of food should have lower slopes in two-patch systems than in systems with more than two patches. This
expectation is obvious in Fig. 3: for any non-zero level of mistake-making, the magnitude of slope depression is highest for the fewest number of patches. To test this, we calculated regression slopes (independent variable: % foragers; dependent variable: % of food in focal patch) for relevant studies. Most of the studies are catalogued in Kennedy and Gray (1993), but we use equilibrium data (i.e., the final 7 points from any time series) from the original studies to calculate slopes, rather than using the ratio technique advocated by Kennedy and Gray (1993). These studies contrast many factors other than number of patches, but we treat them as if all else is equal, simply to see if an effect of number of patches can be detected. The data oppose our expectation: there is a significant negative relationship between slope and number of patches (Fig. 4). We must consider this result preliminary, though, since there are so few studies (i.e., three) that consider more than 2 patches. Also interesting is the number of studies (i.e., 6) contributing slopes greater than one, an effect predicted by no IFD model that assumes identical competitors. Slopes greater than 1 can result when foragers are attracted to the presence of other individuals in a patch, when differences in patch quality are not otherwise perceptible, leading to overuse of good patches.

We suggest that the mechanism involved in slope depression for systems with greater than two patches is akin to that modelled in this paper, but involving an additional variable: information. The difficulty of keeping track of resource and competitor levels in each patch increases as the number of patches do, particularly if moving between patches to acquire this information is costly for the forager. This should lead to more “mistakes” at larger numbers of patches, and therefore to greater deviations from an IFD. In other words, there may be an interaction between number of patches and the probability of mistake-making, such that mistakes are more likely when a forager is required to keep track of more alternative patches. The negative slope in Fig. 4 can be rationalized by examining Fig. 3: if $P_{move}$ increases with number of patches, then lower slopes are predicted for larger numbers of patches. For example, the slope for two patches and a perception limit of 1 is higher than the slope for three patches and a perception limit of three, which itself is higher than the slope for four patches and perception limit of five. As the number of alternative foraging patches increases, so too might the number of mistakes.

The preceding analysis, combined with the results of our simulations, allows for two general conclusions regarding the influence of number of patches on the achievement of an IFD. First, for a fixed non-zero level of erroneous patch choices, departures from an IFD are most easily detected with two patches. Second, the physical and computational difficulty of keeping track of the profitability of alternative patches should increase as do the number of patches, leading to a concomitantly greater level of mistake-making. These two factors should act in opposition, such that the observed departure from an IFD based on number of patches reflects the stronger influence: constant mistake-making predicts a positive relationship between number of patches and slope, while increasing mistake-making predicts a negative relationship.

We conclude with the sobering realization that departures from an IFD may be relatively easy to detect in simple (two-patch) systems, but that in systems more reflective of the real world, with many patches whose differences in quality often do not exceed a twofold range, deviations from IFDs, or even from random, may be difficult to detect statistically. That is, even when the achievement of IFDs under natural conditions may be unlikely, our probability of committing a Type I error (falsely accepting the hypothesis of an IFD, based on a slope whose 95% confidence interval includes one) can be high. The important biological implication of this study is that factors that cause deviations from an IFD are less likely to distort the IFD expectation of equality of intake rates in multipatch systems, except when these factors increase as do
the number of patches. There is some evidence that IFD-distorting influences do increase with number of patches (Fig. 4). Clearly, we need to pay more attention to the foraging mechanisms and consequences to forager distributions associated with variation in the number of alternative patches.

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