OIKOS 54: 33–43. Copenhagen 1989

Diet selection on depletable resources

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Brown, J. S. and Mitchell, W. A. 1989. Diet selection on depletable resources. – Oikos 54: 33–43.

We tested a number of patch use and diet choice strategies using natural populations of kangaroo rats, *Dipodomys merriami*. Patch use strategies included leaving patches: 1) at a fixed quitting harvest rate, 2) after a fixed search time, and 3) after a fixed amount of harvest. The diet choice strategies included: 1) expanding specialist, 2) micropatch partitioning, and 3) resource-specific encounter rates. The predictions of these strategies were couched in terms of forager use of patches containing two resource types and subject to resource depletion. The giving up densitites of kangaroo rats in manipulated resource patches provided the measure of utilization. With respect to patch use, the kangaroo rats use a fixed quitting harvest rate strategy. With respect to diet choice, they incorporate elements of all three diet strategies. This latter result is reasonable given: 1) the biology of kangaroo rats, 2) the characteristics of the resource patches, and 3) that the diet choice strategies are not mutually exclusive.

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Introduction

In this paper we investigate diet selection when a consumer's foraging reduces its encounter rate with its resources. The study of diet selection on depletable resources emerges from combining two classical questions of optimal foraging theory: diet choice and patch use (MacArthur and Pianka 1966). Generally, treatments of diet choice consider an environment in which resource depletion does not occur. The question of interest is which frequencies and types of resources should be included in the forager's diet (Pulliam 1974). Treatments of patch use, on the other hand, consider only a single, patchily-distributed resource which is assumed to deplete as it is foraged. The question of interest is when should a forager leave its present patch and seek another (Charnov 1976; for more complete considerations of models and tests of diet choice and patch use see Krebs et al. 1983, Pyke 1984, Stephens and Krebs 1986 and references therein).

Realistically, many foragers face an environment containing several resource types distributed together in patches [e.g. desert rodents (Brown et al. 1979), grazing and browsing herbivores (McNaughton 1979, Belovsky 1981), herbivorous and coral-eating reef fishes (Lobel and Ogden 1981, Lewis 1985)]. In these systems, the diet choice and patch use of foragers should simultaneously be subject to natural selection.

Several theoretical treatments have considered diet choice in a patchy environment. Heller (1980) simulated on computer several diet choice strategies to calculate the relative payoffs to each. Holt and Kotler (1987) considered the effects of several forager patch leaving rules on the indirect interactions between the resource species within a patch. At least two phenomena emerge from these theoretical treatments that differ from the predictions of classical diet choice and patch use models. First, the patch leaving rule of the forager may generate a negative interaction between two resource species. As a result of this short-term apparent competition (sensu Holt and Kotler 1987), increasing the density of one resource type within a patch can increase the

Accepted 29 May 1988

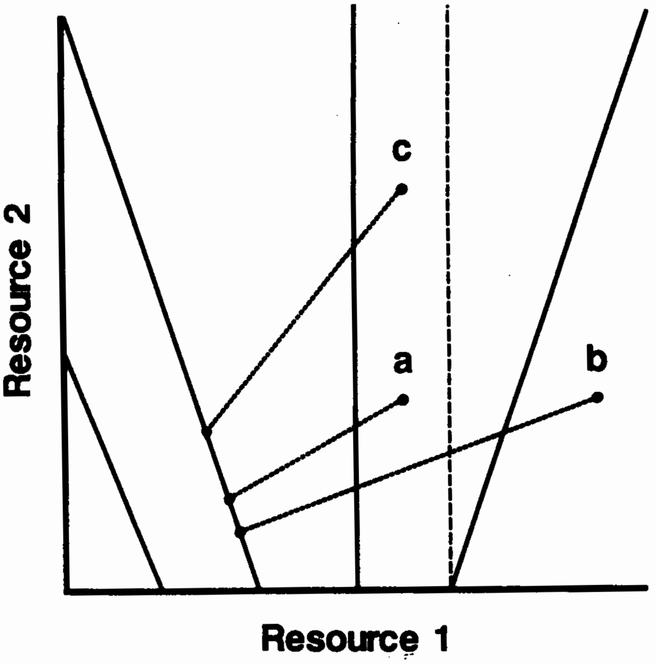

Fig. 1. Equal quitting harvest rate lines and depletion trajectories in the state space of resource densities. Solid lines give combinations of resource densities such that harvest rates are constant. Lines further from the origin correspond to higher harvest rates. The lines assume that resource 1 and 2 are perfect substitutes and that foragers harvest all encountered items of 1 and 2. The vertical solid-line corresponds to a harvest rate of b/h_2 (see text for definitions of b and h_2). To the left of this line, harvesting resource 2 increases the forager's average harvest rate and equal rate lines have negative slope. To the right, harvesting resource 2 decreases the forager's harvest rate and equal rate lines have positive slope. The dashed line is the equal quitting-harvest-rate line of a forager that specializes on resource 1 whenever its quitting harvest rate is to the right of the vertical solid-line. The three points (a, b and c) are initial patch resource densitites. The dotted lines are the depletion trajectories of a generalist forager that has equal attack rates on resource 1 and 2. If the forager's quitting harvest rate lies left of the vertical solid-line, then increasing the density of resource one (a → b) decreases the giving up density on resource 2, and increasing the density of resource 2 (a → b) decreases the giving up density on resource 1 – this is short-term apparent competition (Holt and Kotler 1987).

per capita mortality rate of the other. Second, for the forager, neither a strict specialist nor generalist diet is necessarily optimal. Over a large range of prey densities and patch distributions, the diet which maximizes net energy gain per unit time requires first specializing and then later generalizing (the expanding specialist strategy of Heller 1980; Holt and Kotler 1987). Under such a strategy the forager has a partially selective diet.

We field-tested the predictions of three patch use strategies and the predictions of three diet choice strategies, including those which can result in the two aforementioned phenomena. The three patch use strategies include leaving patches: 1) at a fixed quitting harvest rate, 2) after a fixed amount of time has been spent searching for resources, and 3) after a fixed amount or value of resources has been consumed. The first diet choice strategy is the expanding specialist and it is drawn from Heller (1980) and Holt and Kotler (1987). The second diet choice strategy considers the effects of patch use on diet choice when the foragers detect patchiness on a smaller scale than the researchers. The third diet choice strategy considers a generalist diet when the forager's within-patch per capita encounter-rates for the two resource types differ.

We tested the predictions of the above theories at a Sonoran Desert site by measuring the foraging behavior of *Dipodomys merriami* (Merriam's kangaroo rat) in manipulated resource patches containing two resource types (husked and unhusked millet).

Patch use

In this section we consider several patch leaving rules and their testable consequences for the two resource types. In developing the predictions to be field tested, we make the following assumptions. 1) The forager views the two resource types as perfect substitutes (sensu Rapport and Turner 1977, Tilman 1982); i.e. the value to the forager of consuming an additional resource of type 2 is always a constant fraction, say b, of the value of consuming an additional resource of type 1. 2) The forager may have a different encounter rate, a_i, and handling time, h_i, for each of the two resource types $i = 1,2$. 3) The forager's handling time and area of attack (Hassell 1978) for each type are constant and independent of resource density or patch. 4) Within a patch, resources are distributed randomly and the forager's search is random. Thus, the instantaneous harvest rate of a forager within a patch is described by Holling's disc equation (Holling 1965, Murdoch and Oaten 1975):

$$Q = \frac{a_1R_1 + a_2bR_2}{1 + a_1h_1R_1 + a_2h_2R_2} \tag{1}$$

where a_i is area of attack, h_i is per capita handling time, R_i is remaining resource density (for $i = 1,2$), and Q is the forager's harvest rate in units of prey type 1 per unit time. 5) Resource 1 is preferred to resource 2 in the sense that the ratio of reward to handling time is greater for 1; i.e. $1/h_1 > b/h_2$. 6) Upon entering a patch, the forager can accurately assess resource densities.

We will now consider, in turn, three patch leaving rules: 1) fixed quitting harvest rate, 2) fixed time, and 3) fixed amount. Until the next section, we assume that foragers within patches are generalists and consume all encountered resources.

Fixed quitting harvest rate

Under the above assumptions, a fitness maximizing forager should harvest each patch until the quitting harvest rate just balances the metabolic, predation, and missed opportunity costs of foraging (Brown 1988). In effect, a forager should leave each patch at the same quitting harvest rate, k. By setting (1) equal to k, it is possible to consider those combinations of resource densities, R_1 and R_2, such that harvest rates are equal:

$$R_2 = \frac{a_1 - a_1h_1k}{a_2h_2k - a_2b} R_1 - \frac{k}{a_2h_2k - a_2b} \quad (2)$$

If a forager leaves all patches at the same quitting harvest rate, k, then all of the patch giving up densities should, in the state space of resource-type densities, lie along the straight line described by (2) (Holt 1983). For low quitting harvest rates (low k) the lines of equal harvest rate have negative slopes. As the quitting harvest rate increases ($k \rightarrow b/h_2$), the R_1 intercept of the line shifts outwards and the slope becomes more negative. When the quitting harvest rate equals the ratio of reward to handling time of resource 2 ($k = b/h_2$) then the line becomes vertical. At still larger values of the quitting harvest rate the line takes on a positive slope (Fig. 1; see Holt 1983).

In anticipation of the next section, note that when the line of equal harvest rate is vertical ($k = b/h_2$), the value of R_1 is the critical density of preferred resource in models of diet choice without resource depletion. It is the density of preferred resource when the forager should switch from being a generalist to a specialist (Pulliam 1974). Similarly, this is an important rate when considering diet selection under resource depletion. Whenever the quitting harvest rate is greater than b/h_2 the forager should be selective. Thus, for an optimal forager, the lines of equal harvest rate for $k>b/h_2$ are vertical lines (Fig. 1).

A fixed quitting harvest rate strategy predicts either short-term apparent competition ($k<b/h_2$) (Holt and Kotler 1987) or no indirect interactions between resource types within a patch ($k>b/h_2$). When $k<b/h_2$ the equal rate line has negative slope. Thus, increasing the density of resource 1 (or resource 2) will increase the mortality of resource 2 (or resource 1). Or, in other words, increasing the density of resource 1 (or resource 2) will decrease the forager's giving up density on resource 2 (or resource 1). When $k>b/h_2$ the equal rate line is vertical. Resource 2 is not included in the diet and thus, increasing the density of either resource has no effect on the mortality rate of the other resource (see Fig. 1).

Fixed time and fixed amount strategies

A fixed search time strategy is an optimal strategy for a forager when resources are distributed among patches randomly and when the forager cannot, upon encountering a patch, assess the density of resourses (Iwasa et al. 1981). It is not an optimal strategy under assumption 6 above. Under this strategy, the forager spends an equal amount of search time within each patch, and hence, the forager encounters an equal proportion of a given resource type in each patch. Increasing the density of resource 1 (or resource 2) has no effect on the number of resource 2 (or resource 1) encountered. Thus, increasing the density of either resource type has no effect on the mortality rate of the other resource. A fixed strategy predicts that there will be no indirect interaction between the resource types within a patch.

A fixed-amount strategy means that the forager harvests an equal value, say, v, of resources from each patch; i.e. the strategy is to leave a patch when $v = X_1 + bX_2$ where X_1 and X_2 are the amounts of resource 1 and 2 consumed from the patch. If a generalized diet combines with a fixed-amount patch-use strategy then the opposite of short-term apparent competition occurs. Increasing the density of either resource type increases the amount of that resource in the diet. Thus, increasing the density of either resource type decreases (and increases) the mortality rate (and giving up density) of the other resource.

Diet choice

Now, we consider a number of diet strategies which lead to patterns of selectivity within a patch when resource depletion occurs. In this section, we assume that the forager is using its optimal quitting harvest rate strategy. The case where the quitting harvest rate is greater than the ratio of benefit to handling time of resource 2 ($k>b/h_2$) is easy to dispense with. Under these quitting harvest rates, the optimal diet is to consume only resource type 1. In what follows we will consider only the case where $k<b/h_2$. We will consider, in turn, three diet strategies: 1) expanding specialist (Heller 1980, Holt and Kotler 1987), partitioning of a patch into micropatches, and 3) generalist diet when the foragers' attack rate differs between the two resources, $a_1 \neq a_2$. (For the first two strategies, we assume that the predator has the same attack rate for each prey type; $a_1 = a_2$.) Unlike the patch use strategies of the previous section, these diet strategies are not mutually exclusive.

Expanding specialist

The diet of the expanding specialist includes both a specialist and a generalist component. Under this strategy, the forager consumes only resource 1 when its instantaneous harvest rate is greater than the ratio of benefit to handling time of resource 2; i.e. when $R_1 > b/a_1(h_2\text{-}bh_1)$. At lower instantaneous harvest rates, the forager generalizes and consumes all encountered resources of type 1 and 2 (Heller 1980). This strategy maximizes the forager's instantaneous harvest rate in the patch. Above the critical value of R_1, the forager maximizes its instantaneous harvest rate by specializing on resource 1, below this critical value the forager maximizes its instantaneous harvest rate by generalizing (Holt and Kotler 1987). Such a foraging strategy leads to a specific depletion trajectory in the state space of resource densities. Above the critical density of re-

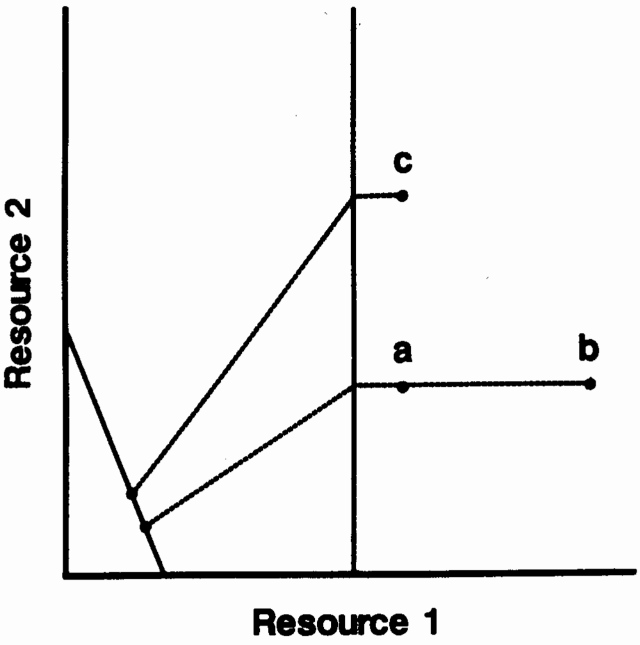

Fig. 2. Depletion trajectories (dotted lines) of the expanding-specialist diet-strategy in the space of resource densities. Under this strategy, the forager selects a diet that maximizes its instantaneous harvest rate. To the right of the vertical equal-harvest-rate line (i.e. the line where k = b/h_2), the forager specializes and the depletion trajectories are horizontal. To the left, the forager generalizes and the trajectories are straight lines toward the origin. Increasing the density of resource 1 and 2 (a → b, and a → c, respectively) increases and decreases, respectively, the proportion of the depletion trajectory which lies in the region of specialization.

source 1 the trajectory is a horizontal line, below the critical density the trajectory is a straight line towards the origin (Fig. 2).

The expanding diet strategy is not necessarily the forager's optimal diet. Consider the case of a single forager in the patch throughout the depletion trajectory. The marginal cost of consuming an item of resource 2 is the quitting harvest rate k. The marginal benefit of consuming an encountered item of resource 2 is the ratio of benefit to handling time, b/h_2. By assumption, $k > b/h_2$ and the forager should consume all encountered items of resource 2 regardless of the current density of resource 1. Whenever a single forager, over the course of the depletion trajectory, has sole proprietorship of the patch and whenever the quitting harvest rate is less than the ratio of benefit to handling time of resource 2 then the forager should generalize. Regardless of the initial density of resource 1, the depletion trajectory will be a straight line towards the origin. For this case, maximizing the instantaneous harvest rate does not maximize the average harvest rate in the patch.

Holt and Kotler (1987) consider the case where a forager is one of many depleting the resources of a given patch. Under these conditions, a single forager contributes little towards patch-resource depletion. With many foragers in a patch, the marginal cost of consuming resource 2 is the current instantaneous harvest rate and the marginal benefit of consuming resource 2 remains the ratio of benefit to handling time of resource 2. Whenever the instantaneous harvest rate is greater than b/h_2, the foragers should consume only resource 1. With many foragers in a patch the expanding specialist is the optimal diet strategy (Mitchell, unpubl.).

What is the effect of increasing resource abundance on the forager's diet selectivity? If the density of resource 1 remains below its critical value then both resource types should be present in the diet in the same proportions as their initial abundances (assuming equal attack rates). Increasing the densities of either resource will have no effect on the forager's selectivity. Now, consider the case where the initial density of resource 1 is above its critical value. Because the forager at first specializes and then generalizes, the frequency of resource 2 in the forager's diet will be less than resource 2's initial frequency in the patch. The forager will exhibit a partially selective diet for resource 1. The more of the depletion trajectory which lies in the region of specialization the greater will be this selectivity (Fig. 2).

The nature of the depletion trajectories leads to the following predictions. Increasing the density of resource 1 will increase the forager's selectivity. This is because more of the depletion trajectory now falls in the region of specialization. Increasing the density of resource 2 will decrease the forager's selectivity. This is because more of the depletion trajectory now falls in the region of generalization (see Fig. 2). Along a depletion trajectory, selectivity should decline. At early stages of the depletion trajectory (characterized by specialization) the forager's selectivity should be great (almost no resource 2 consumed). At later stages of the depletion trajectory (characterized by generalization) the forager should exhibit little to no selectivity (all encountered items of resource 2 consumed).

Micropatch partitioning

Under micropatch partitioning, the forager is able to perceive and respond to random spatial heterogeneity of resource abundances within the patch. Such a strategy is of particular interest when foragers are able to perceive patchiness on a smaller scale than measured by the researcher. In effect, the forager is able to subdivide the patch into a number of micropatches. Assume that the patch abundances of the two resources are distributed randomly within the patch. If so, then the distribution of resources among micropatches will be multinomial. A forager should now harvest each micropatch to the optimal quitting harvest rate. In developing this foraging strategy, we assume that the forager is a generalist and consumes all encountered resources and that the forager's attack rates for the resource types are the same. Under these assumptions all micropatch depletion trajectories are straight lines toward the origin.

Within the state space of resource densities, patch resource abundances are no longer represented by a

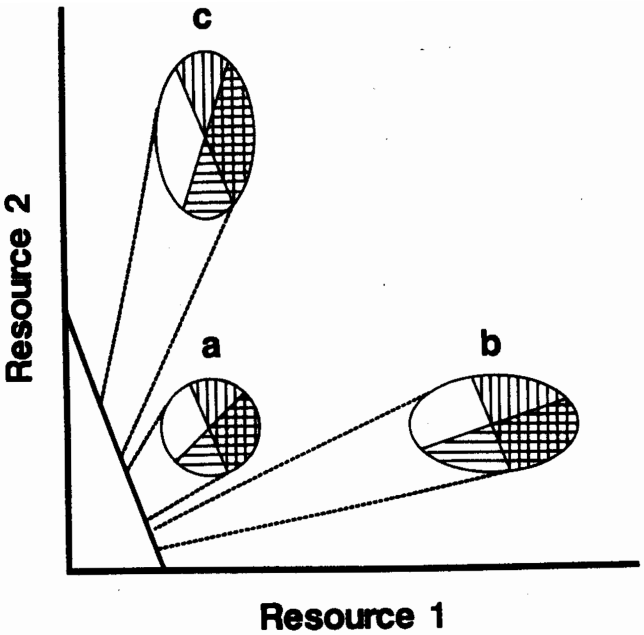

Fig. 3. Depletion trajectories (in the state space of resource densities) when micropatch partitioning occurs. The circles and ellipses give the expected distribution of resources among micropatches when initial patch densities of resource 1 and 2 are randomly distributed among micropatches. Initial conditions "b" and "c" relative to "a" show the results of trebling the initial patch densities of resource 1 and 2, respectively. The circles and ellipses have been scaled so as to represent the same standard deviation from the mean. The dotted lines give the range of depletion trajectories that result from the micropatches of a given patch. Within a circle or ellipse, horizontal hatching indicates micropatches with above average proportions of resource 1, and vertical hatching indicates micropatches that are considered to be of above average quality by foragers with the given equal quitting-harvest-rate line (the solid line). Note that most of the patches that are considered above average by the forager also have an above average proportion of resource 1. This results in a patch-wide partial-selectivity for resource 1 even though foragers generalize within each micropatch.

single point but by a cloud of points encompassing the range of density combinations found among micropatches (Fig. 3). Within each micropatch, the forager is a generalist and shows no selectivity for resource 1. However, patches which on average have a higher density of resource 1 will be foraged to a lower overall density of resources. This is because the slopes of the equal rate lines are more negative than –1. A greater proportion of prey will, on average, be harvested from micropatches that are rich in resource 1 than from micropatches that are rich in resource 2. The harvesting of each micropatch to the equal rate line will result in a net selectivity for resource 1 in the patch as a whole.

Selectivity within the patch increases with variance in prey abundances among micropatches and decreases with the length of the depletion trajectory. The greater the variance the greater the forager's bias towards micropatches with rich abundances of prey 1. And, the longer the depletion trajectories the more dilute are the effects of initial conditions (Fig. 3).

The nature of the depletion trajectories and the random distribution of prey among micropatches provide two predictions. First, increasing the density of either resource type will decrease the forager's partial preference. This is because an increase in resource abundance increases the length of depletion trajectories but leaves unchanged the per-resource-item variance among micropatches – in a multinomial distribution, the ratio of variance to mean is $(1–1/r)$ where r is the number of micropatches. As patch resource abundance increases (while holding the quitting harvest rate constant), the lengths of the depletion trajectories increase proportionately faster than the mean and variance of micropatch resource abundance; hence, patch selectivity declines.

Second, along the aggregate depletion trajectory of the entire patch selectivity should decline. In fact, between successive points along the aggregate trajectory the selectivity for prey 1 should decline and then actually reverse itself to a selectivity for prey 2! The selectivity for prey 2 is the result of cropping the respective micropatches to an equal harvest rate. As harvest rate declines, the successive equal rate lines have larger slopes (less negative) (Fig. 1). This means that the relative value of prey 2 to prey 1 is higher at lower harvest rates. Thus, in foraging micropatches from one equal rate line to the next there should be a greater proportion of prey 2 harvested than prey 1.

Generalist diet with unequal encounter rates

Assume that there is no micropatch partitioning and that throughout the depletion trajectory the forager consumes all encountered resources. The forager can still be partially selective for resource 1 if its attack rate on resource 1 is higher than that on resource 2; i.e. $a_1 > a_2$. Differential attack rates may result from resource crypticity, size, and other resource characteristics such as texture, odor, and shape (Pulliam and Brand 1975, Pulliam 1985). The forager will always show a selectivity for resource 1 that equals a_1/a_2. This selectivity is independent of increasing the density of either resource type and is independent of position along the depletion trajectory. All depletion trajectories are non-linear and bowed upwards from the straight line towards the origin.

How can this diet selectivity be measured by the forager's patch giving up density? Upon abandoning a patch, the forager(s) will have devoted some time, t, to searching for resources. Now, recall the assumptions that the attack rates per resource item are constant and that all encountered resources are consumed. Thus, the number of resources remaining in the patch (the foragers' giving up density), N_1 and N_2 respectively, following t units of search time is:

$$N_1 = R_1 EXP[-a_1 t] \quad (3a)$$
$$N_2 = R_2 EXP[-a_2 t] \quad (3b)$$

where R_1 and R_2 are the initial densities of resource 1 and 2, respectively. Taking the natural logarithm of (1a) and (1b) and rearranging yields expressions for a_1 and a_2. The ratio of these yields:

$$a_2/a_1 = \log[N_2/R_2]/\log[N_1/R_1] \quad (4)$$

The right hand side of (4) should remain constant along depletion trajectories and in response to increasing the densitities of either resource. Furthermore, rearrangement of (4) gives the measure of selectivity, S, which we shall use for the experiments to follow:

$$S = a_1/(a_1 + a_2) \quad (5)$$

S can vary from 0 to 1. S greater than 0.5 indicates partial selectivity for resource 1. Finally, S will usually be normally distributed (Manly 1974, Chesson 1983; see Colton 1987 for an application of this selectivity measure).

Methods

The predictions of the preceding theories of patch use and diet choice have been stated in terms of how patch giving up densities and selectivities change in response to altering the densities of two resource types. We field-tested these predictions by manipulating resource patches to measure the diet choice of Merriam's kangaroo rat (*Dipodomys merriami*) on depletable resources. Patch use and diet choice were measured over a five day period (12–16 February 1986) at a Sonoran Desert site near Tucson, Arizona, USA. The habitat was a uniform creosote (*Larrea* sp.) flat and during the period of the experiment the only nocturnally-active granivorous rodent was the one species of kangaroo rat (see Brown 1986 for a detailed description of the study site).

We established two experimental grids. Each grid was a 4×4 array of stations with 50 meters spacing between stations. At fifteen of the sixteen stations, two resource patches were established side by side in the open microhabitat for a total of 60 resource patches (2 grids × 15 stations × 2 patches). Each resource patch consisted of an aluminum tray (45×45×2.5 cm deep) filled with measured quantities of two seed types mixed into 3 l of sifted dirt. The spacing between stations discouraged individual kangaroo rats from foraging at more than one station (see Brown 1986). The mixing of seeds into dirt approximates a random distribution of prey. The Holling's disc equation provides an excellent fit to laboratory measurements of kangaroo-rat harvest rates from these resource patches (Brown, Valone and Kotler, unpubl. data).

We selected husked and unhusked millet as our two resource types. Millet is readily accepted by kangaroo rats, and, while it is larger than average, millet falls within the range of seed sizes normally encountered. The selection of resource types insured that the two were perfect substitutes to the kangaroo rats. (Kangaroo rats while foraging in these patches husk the millet before returning to their burrows [Brown, pers. obs.].) Furthermore, we assumed that husked millet would be preferred to unhusked millet since it should require a shorter handling time; i.e. husked millet is resource 1 and unhusked millet is resource 2. For these animals, handling time includes the time required to retrieve an encountered seed from the dirt, husk it (if necessary), and pouch it (kangaroo rats have external fur-lined cheek pouches which they use to transport seed to their caches).

Resource patches received from 0–3 "scoops" of husked and unhusked millet. A scoop of husked millet contains 3.39 grams of husked millet (546 seeds at 6.21 mg per husked millet seed). A scoop of unhusked millet contained 2.71 grams of unhusked millet (406 seeds at 6.68 mg per unhusked millet seed) and 0.29 grams of husked millet (47 seeds). (The scoops of unhusked millet contained husked millet because loss of husk in commercial millet is an irreversible "mutation".) At greater than three grams of seeds, these resource patches are of high quality relative to natural seed densities and availabilities (Price and Reichman 1987).

We assigned 15 combinations of resource densities to pairs of patches at different stations: 1) 1–0 and 0–1, 2) 2–0 and 0–2, 3) 3–0 and 0–3, 4) 1–0 and 1–2, 5) 1–1 and 1–3, 6) 2–0 and 2–2, 7) 2–1 and 2–3, 8) 3–0 and 3–2, 9) 3–1 and 3–3, 10) 0–1 and 2–1, 11) 1–1 and 3–1, 12) 0–2 and 2–2, 13) 1–2 and 3–2, 14) 0–3 and 2–3, and 15) 1–3 and 3–3. The two numbers separated by a hyphen denote the number of scoops of husked and unhusked seeds within a patch. The pairs of hyphenated numbers denote the initial patch densities for each tray at a station. Each station of a grid received a different combination and combinations were replicated over grids and nights. The amount of each resource type within patches at a station was arranged so that, in general, the density of one resource type was held relatively constant between patches while the density of the other type was varied. For combinations 4–9, one tray represents a large increase in the density of unhusked millet while for combinations 9–15, one patch represents a large increase in the density of husked millet.

We did not vary over night the initial seed densities of patches at a station. This provides data from the same animals foraging from the same initial densities which can be used to estimate depletion trajectories. In addition, this design probably assists the kangaroo rats in developing an accurate assessment of initial patch seed densities. Similar experiments with these patches suggest that the kangaroo rats can, on a nightly basis, make accurate assessments of prey density (Valone and Brown, unpubl.). Furthermore, because this study was sandwiched between an ongoing project, the kangaroo

Tab. 1. A test for short-term apparent competition. A comparison of trays at a station to see whether increasing the density of husked seeds (or unhusked seeds) decreases (–) or increases (+) the giving up density on the other resource type. Entries under "–" (or "+") indicate that increasing the density of one resource type increases (or decreases) the per capita mortality rate of the other. Sign tests show that the two resource types exhibit short-term apparent competition.

Date	↑ Husked		↑ Unhusked	
	–	+	–	+
12	7	1	6	5
13	10	0	10	0
14	12	0	11	0
15	11	1	11	0
16	10	1	8	3
Total	50	3***	46	8***

*** $p<0.001$

rats of this study area were very familiar with foraging in these resource patches (Brown 1986).

Each afternoon, the patches were set up with their appropriate initial densities of husked and unhusked millet. These patches were then available to the kangaroo rats throughout the night. Each morning we sifted the remaining seeds from the dirt in the patch. The collected seeds were cleansed of debris, and separated as to husked and unhusked. We measured the kangaroo rats' giving up densities on the two resource types within a patch by weighing the remaining husked and unhusked seeds.

Results

The data for this experiment include initial patch densities of seeds, R_1 and R_2, patch giving up densities, N_1 and N_2, and the selectivities for resource 1 (S, calculated with expression (5)). Out of a possible 150 (5 nights × 30 stations), 134 stations were foraged by kangaroo rats. Because the trays at a station are adjacent, they are foraged by the same individuals, and should be subject to the same metabolic, predation and missed opportunity costs of foraging (Brown 1988). Thus, for purposes of analysis, we will assume that the foragers apply the same patch use strategy to both trays at a station on a given night. In contrast, different stations involve different foragers with different opportunities and costs of foraging. Similarly, different nights should offer somewhat different foraging costs and opportunities. Thus, we will assume that foragers between nights and stations apply different quitting harvest rate, fixed time, or fixed amount strategies.

To determine whether husked millet is the preferred resource, we performed a sign test to see whether the average selectivity value, S, is significantly different from 0.5. Different patches and nights provide the replicates. The analysis shows that S is significantly greater than 0.5 and that husked seeds are consumed in a greater frequency than their initial frequency in the patch ($S>0.5$ in 148 out of 158 replicates, $p<0.001$).

To distinguish between patch use strategies, we compared giving up densities between patches at a station to see whether there is a negative (quitting harvest rate), positive (fixed amount), or no (fixed time) indirect interaction between resource types within a patch. We used those stations where scoops of husked seeds were held constant between stations and scoops of unhusked seeds varied (combinations 4–9) and those stations where scoops of unhusked were held constant between patches and scoops of husked varied (combinations 10–15). At a station, increasing the density of husked (preferred) or unhusked (unpreferred) millet results in a lower giving up density (higher mortality) of unhusked or husked millet, respectively (Tab. 1). Thus, the two resource types exhibit short-term apparent competition and increasing the density of one resource results in increased mortality to the other. The data refute the fixed search time and fixed amount strategies and support the equal quitting harvest rate strategy. The line connecting the giving up densities of the two patches at a station has a negative slope.

We tested two additional predictions of the equal quitting harvest rate strategy by determining whether: 1) the slopes of the equal rate lines have a slope less (more negative) than negative one, and 2) whether the slopes of the equal rate lines increase (become less negative) as giving up densities decline. To test the first prediction, we used pairs of patches at a station to calculate the slope of the equal rate line (slope = $[N_{a2}-N_{b2}]/[N_{a1}-N_{b1}]$ where a and b refer to the two patches at a station) using different stations and nights as replicates. For this test we only used those stations which produce negative slopes. The equal rate lines possess slopes more negative than negative one (70 of 118 slopes are less than negative 1; $p<0.025$, one-tailed sign test). To test the second prediction, we used a regression to see whether the slopes of the equal rate lines decline with giving up density. For the slopes we used the above values and for giving up densities we summed the total remaining seeds at a station ($N_{a1} + N_{a2} + N_{b1} + N_{b2}$). The slope of the equal rate lines decline with giving up density ($y = 1.77–0.0080x$ where y is slope and x is giving up density; $t = 1.69$, $p<0.05$, d.f. = 117, one-tailed test). Support for the two predictions provides additional evidence that the foragers are using an equal quitting harvest rate strategy and that the lines connecting the giving up densitites at a station are equal rate lines. The regression equation can be used to construct the kangaroo rat's set of equal harvest rate lines.

To test the predictions of the diet choice strategies, we determined the effects of initial resource density and giving up density on selectivities. The expanding specialist strategy predicts that increasing the density of preferred resources (or unpreferred) will increase (or decrease) the value of S. The micropatch partitioning

Tab. 2. The effect of initial patch abundances of husked and unhusked seed, and giving up density on diet selectivity. The results are for a step-wise multiple regression. Scoops of husked and unhusked seed, and giving up density (GUD: combined density of husked and unhusked seeds) are the independent variables. Selectivity, S, is the dependent variable. The columns give the partial regression coefficients (b), significance of regression (F_T), significance of improvement of next variable over previous variables (F_I), and the cumulative correlation coefficient (r^2). The variables are listed in order of entry into the regression. The sample size is 158 and the y-intercept is 0.560. S increases with GUD and decreases with scoops of husked and unhusked seed.

Variable	b	F_T	F_I	r^2
GUD (seeds)	3.87×10^{-5}	16.34***	–	0.095
Unhusked (scoops)	-1.46×10^{-2}	13.94***	10.53**	0.15
Husked (scoops)	-1.12×10^{-2}	11.75***	6.41*	0.19

* $p<0.05$, ** $p<0.01$, *** $p<0.001$

strategy predicts that increasing either resource type will decrease S. And, the generalist strategy with different attack rates predicts no change in S in response to changing resource densities. Furthermore, the first two strategies predict that S will increase with increasing giving up density and the last strategy predicts no change in S in response to giving up density. We used a stepwise multiple regression where the independent variables were scoops of husked seeds, scoops of unhusked seeds, and total patch giving up density ($N_1 + N_2$). The dependent variable was selectivity, S. Different patches and nights provided replicates. Only those patches with at least one scoop of each resource type were considered. All three independent variables have a significant effect on S (Tab. 2). Increasing either resource type decreases S and increasing the giving up density (quitting harvest rate) increases S. These data support the micropatch partitioning strategy.

A sign test comparing the value of S between pairs of trays at a station can also be used to examine the effect of initial densities of husked (combinations 9–15) or unhusked seeds (combinations 4–9) on selectivity. As in the previous analysis, increasing the density of either seed type decreases selectivity (22 of 26 comparisons, $p<0.001$; and 17 of 24 comparisons, $p = 0.05$ for increasing husked and unhusked seeds, respectively).

The diet choice strategies make predictions concerning selectivities as the depletion trajectory moves from one equal harvest rate line to the next. The expanding specialist strategy predicts that once past the critical density of resource 1, resource 2 should be consumed in equal frequency to its abundance in the patch. The micropatch partitioning strategy predicts that once the initial variance among micropatches has been exploited, resource 2 should actually be consumed in a greater frequency than its abundance in the overall patch. The generalist strategy with different attack rates predicts that resource 2 will, throughout the depletion trajectory, be consumed in a lower frequency than its abundance in the patch.

To test these predictions, we assumed that the different giving up densities within a patch over successive nights could be considered as different points along the depletion trajectory. In going from a higher giving up density to a lower we could then compare how the ratio of resource 2 in the patch changed. If the ratio of resource 1 to 2 increases, decreases, or remains the same as the giving up densities decline then along that portion of the depletion trajectory the frequency of resource 2 consumed is higher, lower, or equal (respectively) to its frequency in the patch. To test this, we used a stepwise multiple regression where scoops of husked seed, scoops of unhusked seed, and giving up density ($N_1 + N_2$) were the independent variables and the ratio of husked to unhusked seed (N_1/N_2) was the dependent variable (Tab. 3). The first two variables obviously have a significant effect on the ratio of husked to unhusked seed. These variables were included to factor out the effect of different starting conditions on the depletion trajectories. Once these have been factored out, patch giving-up-density still has a significant effect on the ratio. The relationship is positive. As one moves down along a depletion trajectory (lower giving up densities) the ratio of husked to unhusked seeds declines. Thus, all along the depletion trajectories resource 2 is consumed in a lower frequency than its patch abundance. These results support the generalist strategy with different encounter rates.

We performed one more set of analyses which is motivated by the results of the previous analyses. It appears that there is micropatch partitioning and that the attack rate for the husked millet is higher than that for the unhusked millet. Is there any evidence from the data to support the possibility that the expanding spe-

Tab. 3. The effect of giving up density on the ending ratio of husked to unhusked seed. The results are for a step-wise multiple regression. Scoops of husked and unhusked seed have been included as independent variables to factor out the effect of initial conditions on the ending ratio. The ending ratio is the dependent variable. The columns give the partial regression coefficients (b), significance of regression (F_T), significance of improvement of next variable over previous variables (F_I), and the cumulative correlation coefficient (r^2). The variables are listed in order of entry into the regression. The same size is 158 and the y-intercept is 1.36. The ending ratio declines as GUD declines.

Variable	b	F_T	F_I	r^2
Husked (scoops)	0.72	105.1***	–	0.40
Unhusked (scoops)	–0.76	232.9***	215.9***	0.75
GUD (seeds)	3.67×10^{-4}	172.3***	13.5**	0.77

** $p<0.01$, *** $p<0.001$

Tab. 4. The effect of giving up density (combined numbers of husked and unhusked seeds) on selectivity, S, for 1, 2 and 3 scoops of husked seed, respectively. The columns give the partial regression coefficients (b), significance of regression (F_T), significance of improvement of next variable over previous variables (F_I), and the cumulative correlation coefficient (r^2). The variables are listed in the order of entry into the regression. The sample sizes are 55, 47 and 56, respectively. The y-intercepts are 0.588, 0.565, 0.529, respectively. Giving up density has a significant effect on S only when there are initially 3 scoops of husked seed.

Variable	b	F_T	F_I	r^2
1 SCOOP				
Unhusked (scoops)	-2.20×10^{-2}	17.6***	–	0.25
GUD (seeds)	3.06×10^{-5}	11.1***	3.68	0.30
2 SCOOPS				
Unhusked (scoops)	-6.60×10^{-3}	1.21	–	0.03
GUD (seeds)	-8.66×10^{-6}	0.77	0.34	0.04
3 SCOOPS				
GUD (seeds)	6.76×10^{-5}	19.3***	–	0.26
Unhusked (scoops)	-1.32×10^{-2}	10.8**	1.87	0.29

** $p<0.01$, *** $p<0.001$

cialist diet is used at the scale of micropatches? Thus far, the only support for the expanding specialist came from the result that selectivities increase as giving up densities increase. In the expanding specialist strategy this change in selectivities along the depletion trajectory occurs only if the initial density of resource 1 is sufficiently high to merit initial specialization on resource 1. This is most likely to occur in patches with high numbers of scoops of husked seed.

To investigate the possibility that the expanding specialist diet may occur at the scale of micropatches, we ran separate multiple regression analyses for each scoop-level of husked seeds. In these regressions, the independent variables were scoops of unhusked seed (1, 2 and 3) and giving up densities ($N_1 + N_2$) and the dependent variable was selectivities (S). Different patches and nights provided replicates. Three regressions were run (Tab. 4). Within a regression the number of scoops of husked seeds was held constant at either 1, 2 or 3. Only when there are 3 scoops of husked seed is there a significant relationship between giving up density and selectivity (increasing giving up density increases S). This result provides support for the expanding specialist strategy within micropatches.

Discussion

Foraging behavior on two patchily distributed resources leads to richer emergent phenomena than either foraging on a single patchily distributed resource or foraging for two resource types without resource depletion. These phenomena have relevance for the direct and indirect interactions between the two resource types and relevance for the optimal foraging strategy of the forager. With respect to indirect interactions, short-term apparent competition (Holt and Kotler 1987) may promote habitat partitioning and coexistence of resource species (Hanski 1981, Holt 1984). With respect to foraging behavior, the forager combines a decision rule for leaving patches with a diet choice strategy within the patch.

The kangaroo rats foraging for husked and unhusked millet in experimentally manipulated patches imposed a negative indirect interaction between resource types. This result of short-term apparent competition depends, among other things, upon the forager's patch use strategy. A fixed amount strategy and a fixed time strategy impose a positive and no indirect interaction, respectively. Thus, the kangaroo rats appear to use a quitting harvest rate strategy for patch departure. This is the optimal strategy of patch use under very general conditions (see Brown 1988) when the foragers can make a fairly accurate assessment of remaining patch resource abundances. Additional evidence for the quitting harvest rate strategy were also forthcoming from the kangaroo rats. As predicted, when resource 1 is preferred to resource 2 and when the resource types are perfect substitutes to the forager, the slopes of the kangaroo-rat's equal rate lines were less than negative 1, and, as the quitting harvest rate increased, the slopes of the equal rate lines became more negative.

When resources deplete and when there are two resource types available within a patch, a number of diet choice strategies will lead to diets which differ from those predicted by diet choice models on non-depleting resources. Under randomly distributed non-depleting resources, the forager should either have a diet composed of nothing but the preferred resource or a diet with a frequency a_2R_2/a_1R_1 of resource 2, where a_1 and a_2 are the forager's encounter rates with resource 1 and 2 respectively. We considered three diet choice strategies on depletable resources.

The first, expanding specialist strategy, specializes on the preferred resource so long as its density is above a critical value. Below this value the forager consumes all encountered resources (Heller 1980). This is the optimal diet strategy when there are many foragers simultaneously depleting the resources of a patch (Holt and Kotler 1987). The kangaroo rats, as evidenced by a decrease in diet selectivity along depletion trajectories that have high initial densities of the preferred resource, appear to incorporate this strategy in their use of patches.

The second strategy, micropatch partitioning, results in a patch-wide diet biased towards the preferred resource, resource 1. Although the forager may consume all encountered resources, it, on average, biases its search effort towards those micropatches that have a higher than average frequency of resource 1. Micropatch partitioning is optimal for the forager and relevant to the researcher when the forager can detect patchiness at a scale smaller than that measured by the researcher. The kangaroo rats, as evidenced by their decreased selectivity as the abundance of either resource is increased, appear to be able to subdivide the experimental patches into micropatches.

A third strategy on depletable resources is to consume all encountered resources within a patch which cannot be partitioned into sub-patches. Such a forager still has a diet that differs from that of a forager on non-depletable resources. Under depletable resources, the forager has a frequency of resource 2 in the diet which is constantly changing (except in the case where encounter rates are equal for the two resource types); the frequency of resource two in the diet is $R_2EXP[-a_2t]/R_1EXP[-a_1t]$ where t is time spent searching for resources in the patch. This third strategy is optimal when the quitting harvest rate is less than the ratio of benefit to handling time of resource 2 and when there are not many foragers contributing towards patch depletion. The kangaroo rats, as evidenced by a continued selectivity for resource 1 along the lower parts of depletion trajectories, appear to have a higher encounter rate for husked millet than for unhusked millet.

In our study with kangaroo rats, none of the diet choice strategies was rejected in favor of another. Such scientific pluralism, however, is not inconceivable. None of these alternative strategies is mutually exclusive. And, based upon what is known about the biology of kangaroo rats, there is good reason to believe that they should, to a certain extent, incorporate elements of all three into their foraging behavior. The use of the quitting-harvest-rate patch strategy by Merriam's kangaroo rat is, perhaps, to be expected because there is good evidence to suggest that kangaroo rats can accurately assess patch quality (Price 1978) even before actual patch exploitation (Valone and Brown, unpubl.).

With respect to micropatch partitioning, our own observations and evidence from previous researchers (Price 1978, Hutto 1978) suggest that Merriam's kangaroo rats can detect patchiness in seed abundances on a scale smaller than 45×45 cm. In fact, given the small scale patchiness of naturally occurring seeds (Reichman 1984, Price and Reichman 1987) there should be considerable selective pressure for micropatch partitioning.

Kangaroo rats use olfaction to help detect and harvest seeds (Johnson and Jorgensen 1981). Thus, the higher encounter rate with husked millet may be the result of husked millet being more odiferous. However, the larger overall size of unhusked millet may mitigate this effect somewhat.

Finally, the kangaroo rats should use the expanding specialist strategy if other individuals may be contributing to resource depletion within the patch. Live-trapping census data in January and March 1983 suggest that there may have been from 36–60 kangaroo rats active on the two grids (this is probably an underestimate because other individuals at the periphery of the grids may be drawn onto the grids for the duration of the feeding experiments). Thus, there were probably one to several kangaroo rats per station and an individual probably could not expect sole use of the patches at a station. Such a situation should encourage the use of a strategy which maximizes instantaneous harvest rate from a patch. Within those micropatches with sufficient abundance of husked millet the kangaroo rat is encouraged to use an expanding specialist diet.

As a caveat, it is important to mention several other proposed mechanisms of foraging behavior whose predictions were not considered in this study. Simultaneous resource encounter (Waddington and Holden 1979, Engen and Stenseth 1984) can generate several of the phenomena observed. If one of the encountered resource items must be rejected then this mechanism results in a partially selective diet. Furthermore, increasing the abundances of either resource type will increase this selectivity because the incidence of simultaneous encounter will rise. A probability of misidentifying resource type coupled with discrimination time (Hughes 1979) may also result in a diet choice exhibiting patterns of selectivity. Depending upon the nature of this mechanism (obligate vs facultative, for instance) it is possible that recognition time may generate similar predictions to the results obtained here (Kotler, pers. comm.).

We feel that this study has significance at two levels. First, and as already discussed, these results provide experimental evidence for the nature of patch use and diet choice on depletable resources. Second, these results are a contribution towards the workings of the optimization paradigm in ecology. The earlier models of diet choice (Pulliam 1974) and patch use (Charnov 1976) made simple assumptions and derived testable predictions. The general agreement of data with these theories develops confidence in the approach, and refutations of these theories' predictions gives momentum to further theories and studies which incorporate different assumptions and biological factors. By investigating the combined implications of diet choice and patch use, this study is an example of this process. The complex foraging behavior of kangaroo rats appears to be the results of several simple processes working together. In the spirit of this process, we hope that this work motivates the theories of others as much as it was motivated by others' theories.

Acknowledgements – Discussions with R. Holt, B. Kotler and M. Rosenzweig contributed greatly to the development and refinement of the ideas herein. A. Gondor, by traversing many miles and sifting much dirt, provided valuable field assistance. The manuscript benefited from comments by P. Alkon, R. Holt, B. Kotler and J. Powlesland. The Graduate Program Improvement Fund from the Univ. of Arizona and the Mitrani Center for Desert Ecology (Blaustein Inst., Ben-Gurion Univ., Sede Boqer, Israel) provided financial assistance. This is publication # 75 of the Mitrani Center.

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