

# Scale-dependent neighborhood effects: shared doom and associational refuge

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**Abstract** A resource's susceptibility to predation may be influenced by its own palatability and the palatability of its neighbors. We tested for effects of plant chemical defenses on seed survival by manipulating the frequency of palatable and less palatable sunflower seeds in food patches subject to harvest by fox squirrels (*Sciurus niger*) and gray squirrels (*Sciurus carolinensis*). We varied resource distributions at three scales: among stations (aggregates of patches ca. 50 m apart), among patches immediately adjacent to each other, and within patches. When food patches were segregated into high-palatability and low-palatability stations (Experiment 1), seeds suffered greater mortality at stations with high levels of palatable seeds. In the same experiment, within patches, squirrels selected strongly for palatable seeds

over less palatable seeds. When high- and low-palatability food patches were placed together at the same stations (Experiment 2), increasing densities of co-occurring palatable seeds amplified the mortality of less palatable seeds, indicating “shared doom.” When palatable and less palatable seeds were partitioned into micropatches (Experiment 3), associational effects disappeared, as predicted. Furthermore, selectivity in less palatable patches increased as the initial densities of palatable seeds increased, and selectivity in palatable patches decreased as the initial densities of less palatable seeds increased. Foraging theory predicts associational effects among prey that vary in palatability. Our results show how the type and magnitude of associational effects emerge from the interplay among the spatial scale of prey heterogeneity, the diet selection strategy, and the scale-dependent foraging responses of the consumer.

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Giving-up densities

## Introduction

Within heterogeneous environments, foragers navigate patches that vary in their composition of resources. Factors influencing patch residence times include the habitat (Brown 1999; Morris and Davidson 2000), the abundance of foods within the patch (Holt and Kotler 1987; Brown and Morgan 1995), the micropatch arrangement of food (Brown and Mitchell 1989; Schmidt and Brown 1996), and the densities of preferred versus less preferred resources (Brown and Mitchell 1989). The spatial distribution of alternative resources in a landscape may also affect their

consumption by a shared predator. For example, short-term apparent competition (Holt and Kotler 1987), describes how, in a two-prey, one-predator system, the presence of one prey species increases the mortality of a second prey species in the same patch. This can be a behavioral indirect effect whereby the presence of a second prey causes the predator to bias its search effort towards that area, thus increasing mortality rates on the first prey (Brown and Mitchell 1989). Alternatively, the second prey may distract the predator from consuming the first, thus decreasing mortality rates on the first prey (Whelan et al. 2003). We investigate experimentally these predator-mediated indirect effects between prey types via the patch-use behavior of the predator.

Neighborhood effects can occur among resources that differ in palatability (Tahvanainen and Root 1972; Root 1973). A favored resource species may attract the consumer to the patch, and result in increased consumption of a less palatable species, a behavioral indirect interaction among resource species that share a common consumer species known as short-term apparent competition (Holt and Kotler 1987). Other names for this effect are “associational susceptibility” and “shared doom” (Wahl and Hay 1995; White and Whitham 2000). Alternatively, a less palatable resource species may repel the consumer from a patch, and a co-occurring, more palatable resource species may experience reduced consumption. The result is “associational defense” (sensu Bergvall et al. 2006), “associational resistance,” or “associational refuge” (Atsatt and O’Dowd 1976; McNaughton 1978; Wahl and Hay 1995; Hjältén and Price 1997; White and Whitham 2000).

Associational effects may also arise via mechanisms not related to food palatability (Root 1973; Stiling et al. 2003). For instance, the predator of a plant’s herbivore might co-occur with the herbivore’s favored resource. In this case, a plant may experience less damage due to its proximity to neighboring plants that attract predators of the herbivore (Root’s “enemies hypothesis”).

When responding to patchiness (heterogeneity of food resources) within their environment, foragers may employ scale-dependent foraging strategies (Danell et al. 1991; Brown and Morgan 1995; Schmidt and Brown 1996; Johnson et al. 2001). Moreover, a forager may perceive and respond to spatial heterogeneity of resource abundances within a food patch (micropatch partitioning; Brown and Mitchell 1989). In this case, the forager’s ability to differentiate among micropatches of food influences the forager’s effects on neighboring prey. Scale-dependent neighborhood effects have been demonstrated in field experiments with red deer and sheep foraging on grasses and heather (Palmer et al. 2003), fallow deer and hazel branches treated with different levels of tannins (Bergvall et al. 2008), and field voles and mountain hares with birch

and either rowan or aspen (Hjältén et al. 1993). We looked for neighborhood effects at three spatial scales. Our predators were free-ranging fox (*Sciurus niger*) and gray (*Sciurus carolinensis*) squirrels, and our prey were sunflower seeds treated with distilled water (undefended, highly palatable) or oxalic acid (defended, less palatable).

We aimed to show how associational effects such as associational refuge or shared doom emerge from the interplay between the forager’s patch use behaviors and the scale at which two resource species co-occur and vary in abundance. We accomplished this by manipulating the abundances of palatable and less palatable sunflower seeds at scales of (1) within food patches (micropatch), (2) among adjacent patches, and (3) among aggregations (stations) of patches at a site (see below for section on “Hypotheses and predictions”).

## Materials and methods

### Study site and experiment organization

The study was conducted at the Morton Arboretum in Lisle, Illinois, comprising 660 ha of botanic collections, native oak woodlands, coniferous plantings, meadows, and a restored prairie. Four sites, each >250 m apart (to insure visitation by different squirrels at each site), were used for two experiments, and three of those sites were used for a third experiment. The woodland canopy is dominated in three of the sites by oaks (*Quercus macrocarpa* and *Q. alba*), and, in the fourth, by black walnut (*Juglans niger*). Foraging stations (aggregates of food patches ca. 10 cm apart, Fig. 2) were chosen in open woodland areas, next to large-diameter trees to reduce the squirrels’ foraging cost of predation (i.e., perception of their own vulnerability to predators; Thorson et al. 1998). Stations were visited primarily by fox squirrels with occasional visits from gray squirrels. One to three individual squirrels visited a station on any given day (personal observation based on species, sex, and individual physical characteristics). While experiments were run 2 or 3 days per week during the timeframes described below, squirrels did not regularly forage at all of the stations. We discarded days with partial data. Consequently, and especially during times when resources were not scarce (food caches are available to squirrels in winter, and new acorns are available in autumn), several months were required to obtain complete data sets. Data were collected for 8 days between January and June 2006 for the first experiment; for 8 days between June and July 2006 for the second experiment; and for 9 days between August and November 2006 for the third experiment. While overall foraging varied seasonally, the ranking of palatable and less palatable foods tested in our

experiment should not be affected by season. Experiments were preceded by several days of “pre-baiting.”

### Food patch preparation

As demonstrated by Schmidt et al. (1998), fox squirrels find oxalate-treated seeds less desirable than water-treated seeds. We soaked commercially obtained husked sunflower seeds for 2.5 h in either a 10% solution (mass:volume) of oxalic acid (to yield a concentration of ca. 5.3%) or in distilled water. Treated seeds were oven-dried for ca. 1.5 h at 90°C, followed by air-drying for several days before use (see Schmidt et al. 1998). In each of our experiments, food patches consisted of 55 cm × 28 cm × 6 cm plastic nursery pallets filled with 4 l of dry commercial bank sand. Into the sand we thoroughly mixed a pre-weighed amount of sunflower seeds (the initial prey density, or IPD). Food patches were available to squirrels from early morning to late afternoon (times varied seasonally, based on available sunlight), when we sieved the sand to remove uneaten seeds. The seeds were then sorted by color (and by taste when color differences were not apparent) and weighed to obtain each giving up density (GUD, the amount of resources left behind when a forager quits a food patch; Brown 1988).

### Proportions harvested

To examine how the mortality of seeds changes with resource distributions, we measured the proportion of each resource type harvested from our depletable food patches. A forager exploiting such a patch should use the patch until the marginal cost of foraging just balances the marginal benefits of exploitation. For each food patch, we can use the proportion of food harvested ( $1 - \text{GUD}/\text{IPD}$ ) as a measure of the food’s mortality in the face of foragers. The proportion harvested standardizes seed mortality with respect to differing initial prey densities.

### Within-patch selectivity

Partial selectivity ( $S$ ) is the relative, proportional harvest of one resource over another resource. To measure selectivity within a patch we use Manly’s index:

$$S = \frac{\ln(\text{GUD}_1/\text{IPD}_1)}{[\ln(\text{GUD}_1/\text{IPD}_1) + \ln(\text{GUD}_2/\text{IPD}_2)]},$$

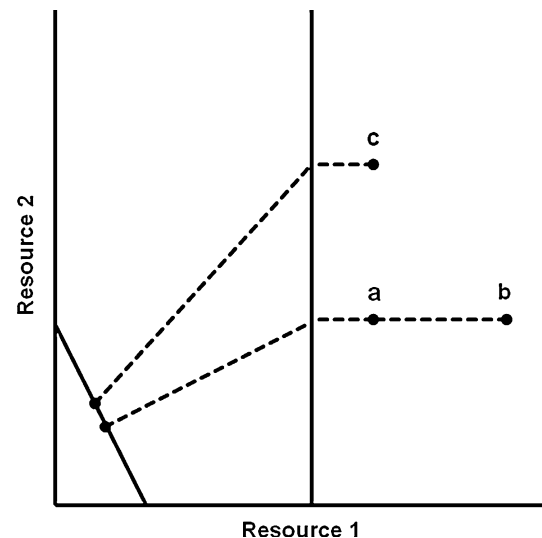
where  $\text{GUD}_i = \text{GUD}$  of resource  $i$  and  $\text{IPD}_i = \text{initial prey density of resource } i$ .  $S$  can vary from 0 to 1, with 0 indicating complete rejection of food 1 and  $S = 1$  indicating complete rejection of food 2.  $S > 0.5$  indicates partial selectivity for resource 1, and  $S < 0.5$  indicates partial selectivity for resource 2 (Manly 1974; Chesson 1983;

Brown and Mitchell 1989). In our experiments, we let palatable seeds represent resource 1, and the less palatable seeds represent resource 2. Selectivity is our second dependent variable of interest in addition to proportion of seeds harvested.

When two foods are mixed randomly within a food patch, and the forager harvests the foods opportunistically, we expect  $S = 0.5$  (because we have no a priori reason to expect that one type of sunflower seed is easier to find than the other, we assume equal encounter probabilities). If the forager rejects some of the less palatable seeds encountered then  $S > 0.5$ . Furthermore, if the squirrels exhibit an expanding specialist diet strategy within the patch (Heller 1980; Brown and Mitchell 1989), then they will be pickier when the patch is rich in palatable seeds and become less selective as the patch depletes (Fig. 1). In this case,  $S$  will decline and become closer to 0.5 as the harvest increases.

### Experiment 1

To test for associational refuge, we randomly mixed 0, 2, 4, or 6 g of less palatable (oxalate-treated) seeds



**Fig. 1** Equal quitting harvest isoclines and depletion trajectories in state space of resource abundances (redrawn from Fig. 1 of Brown and Mitchell 1989). Dotted lines represent depletion trajectories in the space of resource densities for the expanding specialist strategy. To the right of the vertical (equal harvest rate) line, the forager specializes on resource 1. When a critical value of resource 1 is reached (at the vertical line and leftward), the forager expands to generalize, taking all encountered resources. The trajectories become straight lines toward the origin. If the density of resource 1 increases (shifts from  $a$  to  $b$ ), the proportion of the depletion trajectory which lies in the region of specialization also increases. If the density of resource 2 increases (shifts from  $a$  to  $c$ ), the proportion of the depletion trajectory which lies in the region of specialization decreases

(associational food) into each of four patches containing 10 g of palatable seeds (background food). This set of treatments held the initial density of the palatable background seeds constant while varying initial densities of less palatable associational seeds (Fig. 2). To test for shared doom, we randomly mixed 0, 2, 4, or 6 g of palatable seeds (associational food) in each of four patches containing 10 g of less palatable seeds (background food). This set of treatments held the initial density of less palatable background seeds constant while varying initial densities of palatable associational seeds (Fig. 2). Patches containing zero associational seeds represented controls. The four palatable background patches (augmented with less palatable associational seeds) were placed at one station per site in random order that changed daily, and the four less palatable background patches (augmented with palatable associational seeds) were placed at another station ca. 50 m away. Fifty meters was a sufficient distance to measure effects of spatial scale while allowing the same squirrels to visit each station at a site. After 4 days, treatments were switched from one station to the other, for a total of 8 days of data collection. Four replicate sites were used, for a total of 32 patches. We measured seed mortality as the proportion of seeds harvested for each type of seed.

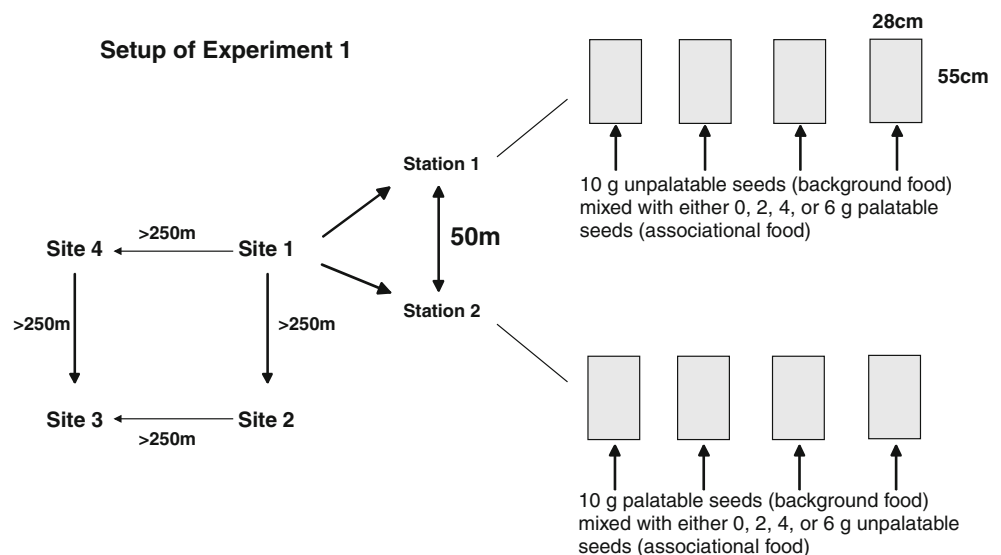
#### Experiment 2

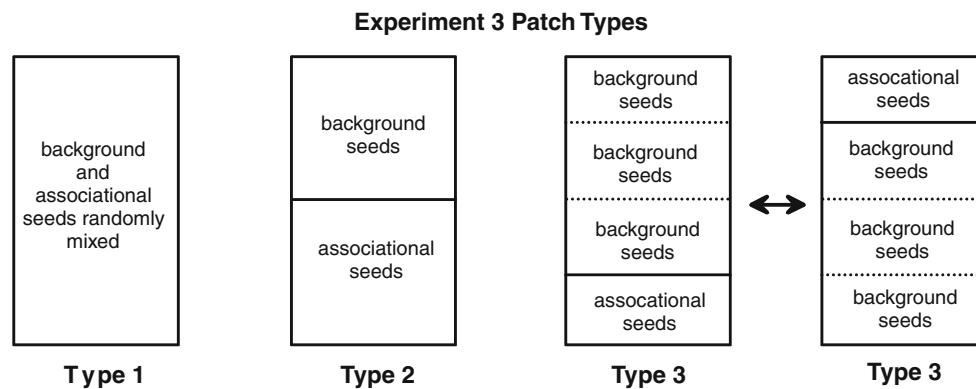
This experiment eliminated the between-stations scale by placing all 8 types of patches used in Experiment 1 at a single station at a site. The same four sites as used in Experiment 1 were employed, for a total of 32 patches. Data were collected for 8 days.

#### Experiment 3

To further test for the interactions of associational effects with scale, we partitioned some patches into micropatches and tested for differences in seed survivorship among three different types of partitioned patches (Fig. 3). We crossed the eight background and associational treatments from Experiments 1 and 2 with three micropatch treatments, for a total of 24 patch treatments. The first micropatch treatment acted as a control, with seeds thoroughly mixed into the sand, as in Experiments 1 and 2. In the second, we mixed the palatable and less palatable seeds into separate halves of a patch. In the third arrangement, we mixed the palatable and less palatable seeds into either  $\frac{3}{4}$  of a patch or  $\frac{1}{4}$  of a patch, with the smaller quantity always occurring in the  $\frac{1}{4}$  micropatch. We always positioned the micropatch at one of the two  $\frac{1}{4}$  end locations, rather than either of the  $\frac{1}{4}$  interior locations, as squirrels can better detect micropatches with distinct boundaries (Schmidt and Brown 1996). Patches were partitioned by placing a wooden divider into the sand. Seeds were mixed into predetermined sections with the divider in place. As natural food patches frequently occur without clear borders, we then removed the divider and smoothed over the surface sand. We used three of the four sites from Experiments 1 and 2, with eight patches placed at a station at each of the three sites. We collected data for three three-day trials, for a total of 9 days. This experiment ran as a variant of a Latin square design; on any given day each of the 24 treatments were present among the 24 trays, and after each three-day sequence a site experienced all 24 treatments. Otherwise, treatments were randomized among stations and sites.

**Fig. 2** Spatial relationships of site, station and patch for Experiment 1. All patches at one station contained one type of background seeds (palatable or less palatable). After 4 days, the treatments were switched between stations





**Fig. 3** The three types of food patches used in Experiment 3. *Type 1* is identical to the patches used in Experiments 1 and 2, where food is thoroughly mixed throughout the tray. *Type 2* is micropatch-partitioned into equal halves, where one food type is placed into each half, and they are not mixed together. *Type 3* is micropatch-

partitioned into a one-quarter section and a three-quarters section, where one food type is placed into each section, and they are not mixed together. Micropatches were always positioned at one of the two  $\frac{1}{4}$  end locations, rather than either of the  $\frac{1}{4}$  interior locations

## Hypotheses and predictions

### *Experiment 1: between-station associational effects*

The survival of seeds of a given species may depend upon the seeds of other species within the background environment. If the squirrels bias their foraging towards the rich stations, then less palatable seeds will suffer shared doom (increased harvest) as a result of being at stations (clusters of patches) where all food patches contain abundant palatable background seeds. Likewise, palatable seeds will enjoy associational refuge (decreased harvest) as a result of occurring at stations with abundant less palatable background seeds (Fig. 2).

### *Experiments 1 and 2: among-patch associational effects*

If varying palatable seeds (associational food) between patches with a fixed-amount of less palatable food (background) causes the squirrels to bias their foraging towards patches higher in palatable foods, then the harvest of less palatable background seeds should increase with the initial amount of palatable seeds (0, 2, 4, or 6 g) within the food patch. Adding palatable seeds to patches with less palatable seeds should result in shared doom.

If adding less palatable seeds (associational food) to a patch with a background of palatable seeds causes less foraging, then the harvest of palatable seeds should decline with the initial abundance of less palatable seeds—an associational refuge. Conversely, even the addition of less palatable seeds may increase the squirrels' perception of patch quality, and so shared doom may still occur but the effect should be less extreme than when palatable seeds vary and less palatable seeds are the background.

### *Experiments 1 and 2: expanding specialist diet strategy*

An expanding specialist diet strategy occurs when a forager starts by selectively harvesting its preferred resource from a patch. Then, as the patch depletes, the forager becomes less selective and forages both the palatable and less palatable foods opportunistically (Heller 1980; Brown and Mitchell 1989). This strategy predicts a partial selectivity for palatable seeds within patches with a high initial density of palatable seeds. Within a patch, this selectivity of greater than 0.5 for palatable seeds should increase with increasing initial densities of palatable seeds and decline as the density of less palatable seeds increases.

### *Experiment 3: micropatch partitioning when palatable and less palatable foods vary within food patches*

Partitioned food patches provide concentrated amounts of each seed type within specified regions of the patches, allowing palatable seeds to be found and less palatable seeds to be avoided more easily. Consequently, associational effects between patches that appeared at the larger scales of Experiments 1 and 2 should be less pronounced or disappear entirely at the micropatch scale. However, within-patch partial selectivities should increase as the palatable food or less palatable food become increasingly concentrated within the patch. A  $\frac{3}{4}$ – $\frac{1}{4}$  partition should lead to greater partial selectivities than a  $\frac{1}{2}$ – $\frac{1}{2}$  partition, which should be greater than an unpartitioned, fully mixed patch.

## Data analysis

We analyzed all of the data with SYSTAT 10 (SPSS Inc. 2000) general linear models (described below). Proportions

of food harvested from patches were arcsine-square root transformed for analyses, while figures show data as proportions. For the general linear models, we treated each food patch as our overall unit of replication. For most analyses there was some nesting of stations into sites, or sites into experimental treatments. Furthermore, as a mixed model design where site and station represent random effects, we would use the appropriate interaction term, when significant, as the error term to test the main effects of background food, associational food, or IPD (see Tables in the Electronic supplementary material, ESM, for details). We did not treat day as a repeated measure for two reasons. First, day was often a blocking variable to complete the design of the experiment. Second, while squirrels may show consistency of behavior at a station across days (or days across stations), we assume that their foraging behavior one day does not nonindependently lock them into a particular foraging behavior the next time they use the patches.

For within-patch comparisons of foraging on the control or oxalate-treated seeds, the data lend themselves to paired  $t$  tests. We treat each patch as a unit of replication for such comparisons.

#### *Proportion harvested, background food*

To test for the effect of varying the associational seeds on the mortality of the background seeds, we used the proportion of background food harvested from patches as the dependent variable and background food type, day, site, and initial prey density (IPD) of associational seeds as the independent variables. In the analysis for Experiment 1, station (nested in site) was included as an independent variable. Site and station were random factors in the models. The analysis for Experiment 3 contained type of micropatch as an additional independent variable.

#### *Proportion harvested, associational food*

To further examine between-patch effects, we tested whether increasing the initial density of a seed type within a patch affects the mortality of that seed type. In this analysis, proportion of associational seeds harvested was the dependent variable, while associational food type, IPD of associational seeds (only 2, 4 and 6 g), day, and site were independent variables. In the analysis for Experiment 1, station (nested in site) was included as an independent variable. Site and station were random factors in the models. The analysis for Experiment 3 contained type of micropatch as an additional independent variable.

#### Within-patch selectivity

If there is no selectivity within patches, all encountered items are harvested, and  $S = 0.5$ . The expanding specialist diet strategy predicts partial selectivity for palatable seeds with a high initial density of palatable seeds, and weak partial selectivity with a high initial density of less palatable seeds. Furthermore, when varying the initial density, selectivity should increase with the density of palatable seeds and decline as the density of less palatable seeds increases. We used selectivity for palatable seeds within a food patch as the dependent variable. Independent variables included background food type, initial prey density (only 2, 4, and 6 g) of associational seeds, day, and site. In the analysis for Experiment 1, station (nested in site) was included as an independent variable. Site and station were random factors in the models. The analysis for Experiment 3 contained type of micropatch as an additional independent variable.

## Results

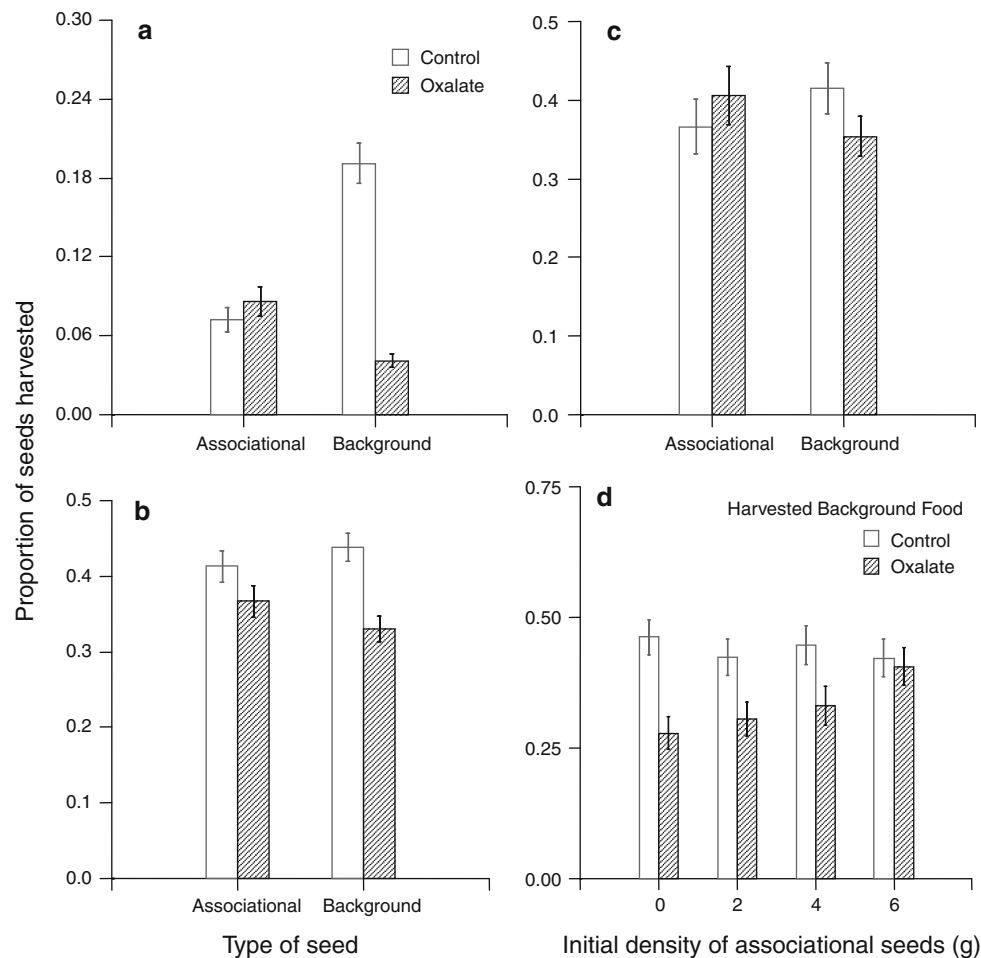
### Experiment 1

#### *Proportion harvested, background food*

The initial density of associational seeds had no effect on the mortality of background seeds; the IPD treatments did not create associational refuge or shared doom. As predicted, patches with palatable background seeds experienced higher mortality than those with less palatable background seeds ( $F_{1,3} = 23.7, P \leq 0.05$ ; Fig. 4a). Effects of day and station (nested in site) were also significant ( $F_{7,222} = 11.2, P \leq 0.001$  and  $F_{4,222} = 7.70, P \leq 0.001$ , respectively; ESM Table 1). Moreover, site interacted significantly with type of background food ( $F_{3,222} = 7.58, P \leq 0.001$ ). The background food type effect remained the same across sites, with a greater disparity at some sites than others.

#### *Proportion harvested, associational food*

Other than significant effects of day ( $F_{7,163} = 3.63, P \leq 0.001$ ), none of the treatments influenced the mortality of associational seeds (ESM Table 1). Interestingly, the less palatable and palatable associational seeds suffered the same mortality, and this was independent of the initial seed density (ESM Table 2). Within patches, a higher proportion of the palatable seeds than the less palatable seeds was always harvested, as confirmed by a paired  $t$  test ( $t_{191} = 8.83, P \leq 0.001$ , Fig. 4a), indicating partial selectivity for palatable seeds within patches (see below).



**Fig. 4** Proportions of seeds harvested (mean  $\pm$  SE) by fox squirrels (*Sciurus niger*) and gray squirrels (*Sciurus carolinensis*). “Control” refers to the palatable sunflower seeds soaked only in water. “Oxalate” refers to the less palatable sunflower seeds soaked in a 10% solution of oxalic acid. **a** In Experiment 1, seeds of both types suffered higher mortality when palatable seeds were the background food (high-palatability stations) than when less palatable seeds were the background food (low-palatability stations). Associational palatable seeds experienced lower mortality than background palatable seeds, and associational less palatable seeds suffered higher mortality than background less palatable seeds. **b** In Experiment 2, background

palatable seeds experienced greater mortality than background less palatable seeds. Less palatable seeds suffered higher mortality as associational food than as background food, and palatable seeds experienced lower mortality as associational food than as background food. Associational less palatable seeds experienced greater mortality than associational palatable seeds. **c** In Experiment 3, background and associational seeds suffered similar mortality. **d** Proportion of less palatable (oxalate) background seeds harvested increased as the initial density of palatable associational (control) seeds increased, indicating shared doom for the oxalate background seeds

#### Within-patch selectivity

Only day ( $F_{7, 158} = 3.97$ ,  $P \leq 0.001$ ) and associational IPD ( $F_{2, 158} = 8.12$ ,  $P \leq 0.05$ ) influenced selectivity (ESM Table 3), with a pattern of increasing selectivity with IPD, particularly for palatable control seeds. Mean selectivity ( $S$ ) for high-palatability patches was 0.717, while mean selectivity for less palatable patches was 0.613. For both patch types in Experiment 1, paired-samples  $t$  tests confirmed that  $S$  was significantly greater than 0.5, ( $t_{91} = 8.45$ ,  $P \leq 0.001$  in palatable background patches and  $t_{94} = 2.84$ ,  $P \leq 0.05$  in less palatable background patches).

As indicated by the significant background food effect, palatable background seeds experienced much lower mortality by being at stations where they were mixed with less palatable food—associational refuge at the between-station scale (ESM Table 1; Fig. 4a). Less palatable seeds suffered higher mortality by being at stations high in palatable food—shared doom at the between-station scale (ESM Table 2; Fig. 4a). There was a nonsignificant trend whereby squirrels were more likely to reject a less palatable seed at a palatable station than at a less palatable station, in a manner suggestive of an expanding specialist strategy. Lending more support for an expanding specialist

diet strategy, selectivity increased significantly with initial density of resources within a food patch (ESM Table 3).

## Experiment 2

### *Proportion harvested, background food*

Day and site effects were significant ( $F_{7, 466} = 26.4$ ,  $P \leq 0.001$  and  $F_{3, 466} = 45.3$ ,  $P \leq 0.001$ , respectively), as were the palatability of background food ( $F_{1, 466} = 33.9$ ,  $P \leq 0.001$ ) and the interaction of associational seed IPD with palatability background food ( $F_{3, 466} = 3.29$ ,  $P \leq 0.05$ ; Fig. 4d). In addition, palatability of background food interacted significantly with site ( $F_{3, 466} = 3.94$ ,  $P \leq 0.05$ ), whereby the pattern at three of the sites was for a greater harvest of palatable seeds, but at the fourth site, the harvest of background food did not appear to differ between palatable and less palatable seeds. Varying the amount of less palatable seeds had no effect on the mortality of palatable background seeds, so again a between-patch associational refuge did not occur as a result of our IPD treatments. The proportion of less palatable background seeds harvested increased with increasing palatable seed IPDs, supporting a between-patch hypothesis of shared doom (Fig. 4d). Palatable background seeds experienced significantly greater mortality than less palatable background seeds (Fig. 4b; ESM Table 4), and patches rich in palatable seeds were foraged more thoroughly than those with high abundances of less palatable seeds.

### *Proportion harvested, associational food*

Less palatable associational seeds experienced significantly greater mortality than palatable associational seeds ( $F_{1, 347} = 3.82$ ,  $P \leq 0.05$ ; Fig. 4b), indicating shared doom for the less palatable seeds in patches with palatable background seeds and associational refuge for the palatable seeds in patches with less palatable background seeds. Day and site effects remained significant, ( $F_{7, 347} = 16.5$ ,  $P \leq 0.001$  and  $F_{3, 347} = 40.7$ ,  $P \leq 0.001$ , respectively). Palatability of associational food interacted significantly with site ( $F_{3, 347} = 3.72$ ,  $P \leq 0.05$ ; ESM Table 5), whereby less palatable associational seeds experienced greater harvest than palatable associational seeds at two of the sites, while at the other two sites, harvest was the same between the two seed types.

### *Within-patch selectivity*

Paired-samples  $t$  tests confirmed that selectivity values did not significantly differ from 0.5 in the palatable background patches (mean selectivity was 0.52). In the less palatable background patches, selectivities were significantly greater

than 0.5 ( $t_{179} = 2.55$ ,  $P \leq 0.05$ ), with a mean of 0.531. The shared doom effect upon less palatable background seeds was, therefore, somewhat moderated by partially selective foraging within those patches. The fact that partial selectivity disappeared in the palatable background patches indicates that selectivity was not influenced by background resource palatability.

Overall, high-palatability patches received more foraging than low-palatability patches (Fig. 4b), less palatable background seeds suffered shared doom from increasing IPDs of palatable associational seeds, and less palatable associational seeds suffered higher mortality by being in high-palatability patches (shared doom), as a between-patch effect. Likewise, palatable associational seeds enjoyed much lower mortality by occurring in low-palatability patches (associational refuge; Fig. 4b).

## Experiment 3

### *Proportion harvested, background food*

Varying the IPDs of associational seeds had no effect on the harvest of the background seeds for either patch type (palatable background or less palatable background). As in the previous experiments, day and site effects were significant ( $F_{8, 169} = 2.62$ ,  $P \leq 0.05$  and  $F_{2, 169} = 96.6$ ,  $P \leq 0.001$ , respectively). Palatable background seeds experienced mortality similar to less palatable background seeds (Fig. 4c; ESM Table 7).

### *Proportion harvested, associational food*

Associational seed mortality was not influenced by the palatability of the associational seed or the type of micropatch. Day and site effects remained significant ( $F_{8, 133} = 2.37$ ,  $P \leq 0.05$  and  $F_{2, 133} = 95.6$ ,  $P \leq 0.001$ , respectively), and the proportion of associational seeds harvested increased significantly with IPD, ( $F_{2, 133} = 5.54$ ,  $P \leq 0.05$ ). However, no significant interaction was found between IPD and type of associational food (ESM Table 8).

### *Within-patch selectivity*

With highly palatable and less palatable food patches side by side but partitioned such that less palatable seeds and palatable seeds were concentrated into different sections of each patch, one might expect the type of background food to affect partial selectivity as a result of the less palatable seeds being easier to avoid. Furthermore, selectivity on palatable seeds should increase as the initial density of palatable seeds increases and decrease as the initial density of less palatable seeds increases (as an effect of

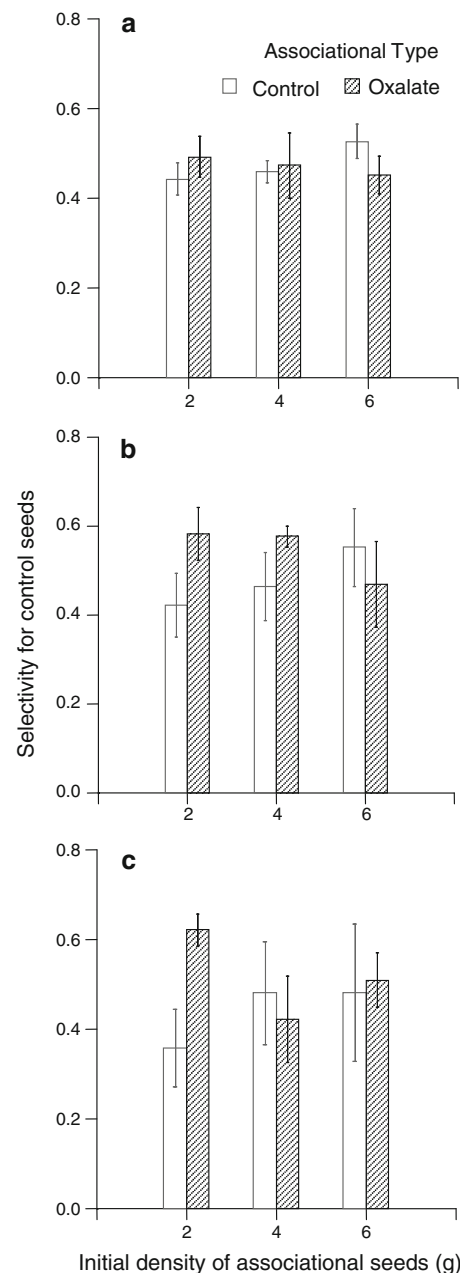


associational IPD and the interaction of associational IPD with background food). Selectivity in less palatable patches increased as the initial densities of palatable seeds increased, and selectivity decreased as the initial densities of less palatable seeds increased in the palatable patches, ( $F_{2, 117} = 5.97$ ,  $P < 0.05$ ; Fig. 5). Furthermore, there was a significant interaction between IPD of associational seeds by background food and micropatch type ( $F_{4, 117} = 2.63$ ,  $P < 0.05$ ; Fig. 5). However, among day, site, background food, infrequent IPD, and micropatch type, none had any effect on within-patch selectivity (ESM Table 9). We conducted a series of  $t$  tests to determine whether selectivity values differed from 0.5. No significant deviations of  $S$  from 0.5 were found in either high- (mean  $S = 0.535$ ) or low- (mean  $S = 0.504$ ) palatability patches. Nor were significant differences found for any of the micropatch types. Selectivities in whole, half, and quarter micropatch divisions were 0.473, 0.548, and 0.536, respectively. Though overall selectivities were close to 0.5 for all micropatch types, they did follow our predictions for changing the initial density of seeds, particularly in the quarter micropatches, as demonstrated by the interaction of associational IPD with background food with micropatch (Fig. 5a, b and c; ESM Table 9).

As predicted, associational effects on either background or associational seeds did not occur when food patches were partitioned into micropatches. In accord with micropatch partitioning, selectivity for the palatable seeds increased with increasing palatable associational IPDs and decreased with increasing less palatable background IPDs (Fig. 5).

## Discussion

The experiments revealed four avenues for associational effects. First, a forager may harvest more thoroughly those patches with high abundances of palatable food than patches with high abundances of less palatable food. All experiments tested for this effect by having either a high level of palatable seeds or a high level of less palatable seeds within a patch. Strong associational effects at this scale occurred in Experiments 1 and 2. In accord with shared doom, a less palatable seed was more likely to be consumed when in a patch with palatable background seeds than one with less palatable background seeds. In accord with an associational refuge, a palatable seed was less likely to be harvested from a patch with a high abundance of less palatable than one with a high abundance of palatable seeds (Fig. 4a, b, c). Any given food item (palatable or less palatable) is more likely to be consumed when in a patch with a background of palatable seeds than in one with a background of less palatable seeds.



**Fig. 5** Selectivity for palatable seeds (mean  $\pm$  SE) in Experiment 3. *Control* refers to the palatable sunflower seeds soaked only in water. *Oxalate* refers to the less palatable sunflower seeds soaked in a 10% solution of oxalic acid. Selectivity on palatable seeds increased with the initial density of palatable seeds and decreased with initial density of less palatable seeds in **a** whole, **b** half–half partitioned, and **c** one-quarter–three-quarters partitioned patches

Second, changing the relative abundance of low- or high-palatability foods within a patch may create associational effects. This effect is similar to that of short-term apparent competition or short-term apparent mutualism (Holt and Kotler 1987). Increasing the relative abundance of palatable food may increase the mortality of the less palatable food (shared doom through short-term apparent

competition), and, on the flip side, increasing the relative abundance of less palatable foods will decrease the mortality of more palatable foods (associational refuge through short-term apparent mutualism). While all three experiments tested for this between-patch effect, it was generally absent or more subtle than the first effect (between clusters of patches differing in background food palatability). Nevertheless, in the second experiment, increasing the relative abundance of palatable seeds in patches with a background of less palatable seeds resulted in shared doom (Fig. 4d).

Third, the way palatable and less palatable foods are aggregated within a patch may affect survival. For example, as an herbivore moves through a sward of vegetation, it may be able to exert greater selection if each plant type occurs as clumps than if sprigs or shoots are inseparably intermixed. For instance, the lip biting of horses, zebras, and rhinoceros is thought to provide a means for smaller scale diet selectivity (Shrader 2003). This form of aggregation within patches has been termed micropatch partitioning (Schmidt and Brown 1996). In our third experiment, micropatches had only minor effects on seed mortality.

Fourth, within-patch associational effects weaken if the forager harvests food opportunistically from a patch. By opportunistic, we mean the forager harvests all encountered food items regardless of palatability. In contrast, a forager may exhibit a partial selectivity within the patch, accepting all palatable food items for harvest and occasionally rejecting less palatable ones. In all experiments, we tested for within-patch partial selectivity and found it to be significantly greater than 0.5 in both patch types (backgrounds of both less palatable and palatable seeds) of the first experiment and in the less palatable background patches of the second experiment. This partial selectivity tends to dampen some of the between-patch associational effects described above. For instance, the partial selectivity for palatable seeds provided less palatable seeds with improved survival when in the presence of high densities of palatable seeds. In Experiment 3, the squirrels showed a much lower tendency to select for palatable seeds over less palatable ones within food patches. Quarter micropatches did provide a sufficiently small scale to change IPDs of associational seeds to affect selectivity (Fig. 5c).

To test for associational defense (refuge), Bergvall et al. (2006) measured the patch residence times of fallow deer foraging among patches of high and low tannin content pellets. In their system, associational refuge is revealed when selectivity is strong between patches and weak within patches. However, selectivity was reversed, and neighbor contrast susceptibility, the opposite of associational defense, occurred. GUDs and/or proportion harvested correspond to the measure of selectivity used by Bergvall et al.

(2006). In the research presented here, significant mortality differences on the background food between “good” and “bad” patches in the first two experiments suggest strong among-patch “selectivity,” leading to associational defense. In an example of associational refuge mediated by voles and hares, Hjältén et al. (1993) found reduced foraging on shoots of birch when they were bundled into stands with less palatable plants. Wahl and Hay (1995) found both associational refuge and shared doom resulting from pairwise sea urchin grazing on host seaweeds and epibiotic plants and animals. Our findings of shared doom and associational refuge, at the among-patches spatial scale, corroborate those of Hjältén et al. (1993) and Wahl and Hay (1995).

A likely explanation for the high selectivities exhibited by squirrels in the first experiment is an expanding specialist diet strategy. When foragers employ this strategy, they begin as specialists on their preferred resource but become less selective as they deplete it to a critical density (the vertical line in Fig. 1). A consequence of separating our treatment types into different stations was the creation of richer neighborhoods (the station with only palatable background seeds), producing pronounced costs of missed opportunities (Brown 1988). This segregation raised the squirrels’ initial selectivity for palatable seeds in the rich neighborhoods, which, in turn, caused the differences in mortality (between less palatable and palatable seeds) to be greater at the highly palatable stations (Fig. 4a). In Experiments 2 and 3, where all patches per site were intermixed at the same station, foraging costs became equal for all food patches at a site, and within-patch selectivity decreased in these experiments. Having high- and low-palatability food patches together diluted the overall richness of the neighborhood, and the density of the palatable seeds fell below a critical value for the squirrels to specialize on them.

Spatial scale can influence diet selection, as seen in sheep choosing their preferred foods only at high pellet lengths (Edwards et al. 1994), and in squirrels exhibiting different mechanisms of selectivity (i.e., related to GUD vs. related to the initial abundance of foods), depending on the spatial scale of food patches (Brown and Morgan 1995). Our research reveals three spatial scales at which a forager can avoid less palatable food. In the first experiment, squirrels could avoid less palatable seeds by choosing stations containing fewer less palatable seeds or by choosing patches with fewer less palatable seeds. The ability to choose highly palatable stations allowed them to be selective for palatable seeds. In the second experiment, squirrels could avoid less palatable seeds only by choosing patches with fewer less palatable seeds. This provided the fewest ways to avoid less palatable seeds, and, as a result, less palatable background seeds experienced shared doom as palatable seed density increased (Fig. 4b). In the third

experiment, squirrels could avoid less palatable seeds at the among-patches and within-patch scales. Consequently, palatable seeds suffered greater mortality than less palatable seeds (Fig. 4c). Bergvall et al. (2008) achieved results similar to those in our third experiment. When mixtures of palatable and less palatable branches were presented in bundles, associational defense was experienced. When the same mixtures were spread out, deer could easily choose palatable branches, and associational effects disappeared.

Neighborhood effects on prey can be precipitated by foraging scale, foraging costs, and diet strategy of the predator. We examined the impact of the palatabilities and relative abundances of two resources on each other's survival at three spatial scales. Our results revealed that, among food patches and among stations of food patches, associational refuge and shared doom can both occur. However, when seeds are partitioned into micropatches, these effects are dampened by the consumer's facility to avoid less palatable resources. The strikingly elevated within-patch selectivity at palatable stations reveals that the consumer's diet strategy intersects with spatial scale and foraging costs to create a large-scale associational refuge for palatable seeds hiding in less palatable stations. Relative abundance of less palatable seeds did not impact the survival of palatable background seeds, as we would have expected of an among-patch effect. However, we have teased apart the environmental contingencies for associational effects and shed some light upon the roles of diet strategy and spatial scale in enhancing, minimizing, and mediating neighborhood effects.

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