

The foraging behavior of granivorous rodents and short-term apparent competition among seeds

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The foraging behavior of a predator species is thought to be the cause of short-term apparent competition among those prey species that share the predator. Short-term apparent competition is the negative indirect effect that one prey species has on another prey species via its effects on predator foraging behavior. In theory, the density-dependent foraging behavior of granivorous rodents and their preference for certain seeds are capable of inducing short-term apparent competition among seed species. In this study, I examined the foraging behavior of two heteromyid rodent species (family Heteromyidae), Merriam's kangaroo rats (*Dipodomys merriami*) and little pocket mice (*Perognathus longimembris*). In one experiment I tested the preferences of both rodent species for the seeds of eight plant species. Both rodent species exhibited distinct but variable preferences for some seeds and avoidance of others. However, the differences in preference appeared to have only an occasional effect on the strength of the short-term apparent competition detected in a field experiment. In another experiment, I found that captive individuals of both rodent species had approximately equal foraging effort (i.e., time spent foraging) in patches that contained a highly preferred seed type (*Oryzopsis hymenoides*) regardless of seed density and the presence of a less preferred seed type (*Astragalus cicer*) in the patches. The rodents also harvested a large proportion of *O. hymenoides* seeds regardless of initial seed density; this precluded a negative indirect effect of *A. cicer* on *O. hymenoides*. But there was a negative indirect effect of *O. hymenoides* on *A. cicer* caused by rodents having a lower foraging effort in patches that only contained *A. cicer* seeds than in patches that contained *A. cicer* and *O. hymenoides* seeds. The indirect interaction between *O. hymenoides* and *A. cicer* thus represented a case of short-term apparent competition that was non-reciprocal. Most importantly, it was caused by the foraging behavior of the rodents. *Key words*: density dependence, foraging behavior, heteromyid rodent, kangaroo rat, seed preference, short-term apparent competition. [*Behav Ecol* 12:467–474 (2001)]

Competition between species occurs when one species negatively affects the population size or growth rate of another species. Ecologists often refer to this interaction as resource competition. However what may appear to be resource competition might actually not be any form of direct interaction. The indirect interaction known as apparent competition (Holt, 1977; Holt and Kotler, 1987) occurs when one prey species negatively affects another prey species because one or both prey have a positive effect on a predator species. This positive effect can be either a numerical increase in the number of predators, an aggregation of predators to a patch of prey, or an increase in the capture and consumption rate of prey. The important point is that one of the prey species induces this positive effect on the predator that causes the predator to exert a negative effect on the other prey species. Apparent competition is distinguished from real competition in that apparent competition does not involve any direct negative interaction between species competing for a limiting resource. However, the consequence of apparent competition, a decrease in the abundance of one or both prey species, resembles the effect that would result from classical resource competition, hence the term “apparent.”

It is necessary to distinguish between long-term and short-term apparent competition because the latter is explained by the behavior of the predator where the former does not nec-

essarily require explicit consideration of predator behavior. Short-term apparent competition arises from an aggregative or functional response of individual predators to the combined density of two prey species. Long-term apparent competition arises from a numerical response of the predator population to one or both populations of the prey species. A numerical response requires a longer period of time to be manifested than do either aggregative or functional responses which can occur within a period of minutes, hours, or the duration of the predator's foraging bout.

More than a decade ago, Holt and Kotler (1987) predicted that interactions between alternative prey species (i.e., short-term apparent competition) should be strongly influenced by the behavior of individual predators. Yet to date there are very few studies of the behavioral causes of apparent competition, despite the fact that the theoretical basis of short-term apparent competition was derived from optimal foraging theory which is widely studied. Holt and Kotler (1987) demonstrated analytically that a negative indirect interaction between prey species, which they called “short-term apparent competition,” could be generated by a shared predator foraging optimally in both its choice of patch and choice of prey. Optimal foraging can produce short-term apparent competition when a predator forages opportunistically (i.e., does not discriminate among prey species) as its instantaneous rate of harvest approaches the average rate of prey yield in an environment that is deficient in prey (Holt and Kotler, 1987). The behavioral sequence that can lead to short-term apparent competition is as follows: a predator enters a patch and begins foraging for prey, it then switches to a second prey species as it depletes the first species, finally it departs when its instantaneous rate of prey capture equals the rate it could achieve in other patch-

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es. A predator will thus spend more time (and capture more individuals of each prey species) in a patch that has both prey species than in a patch with only one prey species. Short-term apparent competition is this decreased survival of one prey species when in the presence of another prey species.

The few studies that have examined predator behavior as a potential cause of either short-term or long-term apparent competition are limited to studies of the prey searching behavior of parasitoids (Settle and Wilson, 1990), predatory mites (Janssen et al., 1998), and big-eyed bugs (*Geocoris punctipes*; Eubanks and Denno, 2000). The first two studies did not explicitly link the predator behavior to an empirical demonstration of short-term apparent competition. The third study, Eubanks and Denno (2000), found that prey mobility was an important factor in causing a positive indirect effect (i.e., apparent mutualism) of pea aphids on the immobile eggs of corn earworms. Big-eyed bugs appear to prefer the mobile pea aphids to the eggs of corn earworm even though the latter are more nutritious. Another notable study is that of Brown and Mitchell (1989). They documented short-term apparent competition between two different types of millet seeds and ascribed its existence to the patch-leaving rule of the heteromyid rodents (family Heteromyidae) that foraged for the seeds. Brown and Mitchell (1989) inferred the existence of the patch-leaving rule from measuring seed predation rates; but they did not directly observe behavior.

Heteromyid rodents harvest seeds from a variety of plant species. Studies of these species have revealed short-term apparent competition, presumably caused by the foraging behavior of the rodents (Veech, 2000; Veech JA and Jenkins SH, manuscript submitted). This effect of rodent foraging could arise via two mechanisms. First, the rodents' response to seed density might induce short-term apparent competition. Heteromyid rodents tend to harvest a greater proportion of seeds from patches with a high density of seeds than from patches with a low density of seeds (Bowers, 1990; Brown, 1988; Mitchell and Brown, 1990; Price and Heinz, 1984). Previous research has shown that heteromyid rodents are more likely to induce apparent competition between two seed species if the mixed-species patches have a higher total density of seeds (both species combined) than the monospecific patches (Brown and Mitchell, 1989; Veech JA and Jenkins SH, manuscript submitted). This would seem to implicate density-dependent foraging as the cause of the interaction, but until now this possibility has not been tested. Density-dependent foraging could result from either a functional response, an aggregative response, or both. A functional response would exist if rate of seed harvest per visit were to increase with the density of seeds in a patch. An aggregative response would exist if the number of seed predators aggregating in a patch were to increase with increasing density of seeds in the patch (Brown and Mitchell, 1989; Holt and Lawton, 1994).

Second, a much greater preference of rodents for one seed species versus another could result in short-term apparent competition. Holt and Kotler (1987) demonstrated theoretically that the presence of a high-quality prey can substantially reduce the survival of a low-quality prey when predators increase their foraging time due to the presence of the high-quality prey and thereby harvest some of the low-quality prey. Therefore, short-term apparent competition among seeds may also be due to seed preferences (i.e., perception of prey quality) and the effect they have on the foraging behavior of the rodents. Heteromyids prefer some types of seeds over others (Longland and Bateman, 1998; Podolsky and Price, 1990; Reichman, 1975). Their preferences are often based on the nutritional content or size of the seeds (Frank 1988; Hendersson, 1990; Jenkins and Ascanio, 1993; Price, 1983; Reichman, 1977). Following the reasoning of Holt and Kotler (1987)

seed preference could affect the occurrence and strength of apparent competition if seed patches with highly preferred seeds tend to attract and retain seed predators for a longer time than patches without highly preferred species. For instance, survival of less preferred seeds (e.g., *Astragalus cicer* seeds) should be lower when they are in a patch with the highly preferred seeds of Indian ricegrass (*Oryzopsis hymenoides*) than when in a patch alone. This effect could occur when a rodent is foraging for seeds of both species and remaining in the mixed-seed patch for an amount of time longer than the time it would spend in a patch that does not have the highly preferred seed species. In this scenario a rodent enters a patch and begins to forage. Whether or not it continues foraging depends on the rate at which it is harvesting seeds and the identity of those seeds. If the rodent is not harvesting any preferred seeds (because there are none in the patch) then it may quickly leave the patch. But if the rodent is harvesting preferred seeds then it may continue to harvest those seeds and also begin harvesting less preferred seeds before departing the patch. This foraging behavior, thus, leads to a negative indirect interaction between the two seed species. That is, both seed species suffer greater predation in the mixed-species seed patch than in single-species seed patches because the rodent spends more time in the mixed-species patch and harvests more seeds of each species from those patches. In general, the presence of a highly preferred seed species, such as *O. hymenoides*, should decrease the survival of seeds of other preferred species and vice versa.

The purpose of this study was to examine the effects of seed density and seed preference on the foraging behavior of the heteromyid species, Merriam's kangaroo rats (*Dipodomys merriami*) and little pocket mice (*Perognathus longimembris*). In particular, I tested whether behavior influenced by seed preference and seed density may explain apparent competition measured in the field.

METHODS

All of the rodents used in the experiments were captured at Nightingale Flat (39°50'30" N, 119°00'10" W) about 80 km NE of Reno, Nevada, USA. The rodents were captured between January and May 1999 and kept in captivity for as long as necessary to complete the experiments (usually less than 4 weeks) and then released at the site of capture. The rodents were maintained on a diet of mixed bird seed (mostly millet) provided ad lib and lettuce. They were housed in small plastic cages (47 × 26 × 20 cm) filled with a sand substrate and a can for shelter. All rodents were kept in an animal holding facility on a 12L:12D photoperiod at 19–23°C. Most of the rodents were used in only one of the experiments described below.

Seed preference

I measured the preferences of 16 *Dipodomys merriami* and two *Perognathus longimembris* for seeds of eight different plant species. Of the eight species, the following six were found at the study site: *Bromus tectorum* (cheatgrass, BRO), *Oryzopsis hymenoides* (Indian ricegrass, ORY), *Lupinus* sp. (LUP), *Penstemon* sp. (PEN), *Sphaeralcea coccinea* (globemallow, SPH), and *Stanleya pinnata* (prince's plume, STA). *Astragalus cicer* (cicer milkvetch, AST) was not found at the study site but its close congener (*A. lentiginosus*) was, so *A. cicer* was used as a substitute. *Panicum miliaceum* (millet, PAN) was not found at the study site but it has been widely used in studies of rodent foraging behavior, hence its inclusion in this study. Each rodent was fasted for 12 h prior to the start of its trial. The trials were conducted in small indoor arenas (70.7 × 70.7 × 50 cm) each of which had a sand substrate and a nest box in one

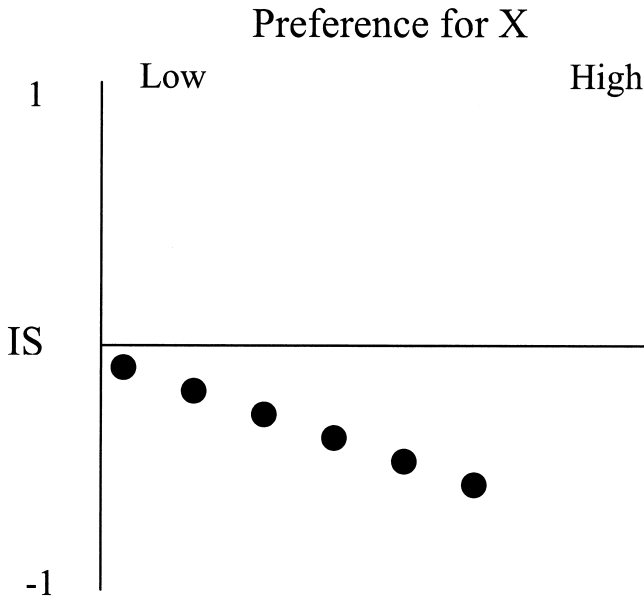


Figure 1

The relationship between seed preference and the indirect effect of one seed species on another ($IS_{A \rightarrow B}$ or $IS_{B \rightarrow A}$) for six seed species (black dots). Seeds of species that have low preference rankings should exert only a small negative indirect effect on a more preferred species such as *Oryzopsis hymenoides* ($IS_{X \rightarrow ORY}$) and should receive only a small indirect effect ($IS_{ORY \rightarrow X}$) from *O. hymenoides*. Seeds of species that have higher preference rankings both exert and receive a more negative indirect effect. This relationship between seed preference and the strength of short-term apparent competition may arise if increased seed preference translates into increased amount of time spent foraging in the mixed-seed patch.

corner. Each trial began at 1800 h of Day 1 and lasted until 0900 h of Day 3. During the 39-h trials, each rodent had free access to a cafeteria-style seed tray that contained 1.0 g of each of the eight seed species. The seed tray was a small wood board (38 × 18 cm) with eight plastic petri dishes (diameter 8 cm) glued to its surface. The dishes were adjacent to one another and formed two rows of four. Each seed species was randomly assigned to one of the dishes. The seed tray was placed in the center of the arena. At the end of each trial I collected all intact seeds that remained on the seed tray, in the sand, and in the nest box. I then reweighed the seeds to determine the mass of seeds that had been consumed by each rodent.

In subsequent analyses, I used both absolute seed preference (mass of seeds consumed) and relative seed preference (mass of seeds of species j consumed/total mass of all seeds consumed). The preference data were used to examine the relationship between the strength of the ORY/X indirect interaction (i.e., apparent competition between seeds of ORY and species X) and the preferences of heteromyid rodents for seeds of species X where X represented AST, LUP, PAN, PEN, SPH, or STA. I measured the strength of the indirect effect of ORY seeds on each of the other species ($IS_{ORY \rightarrow X}$) as:

$$IS_{ORY \rightarrow X} = PSS_{\text{mix}} - PSS_{\text{single}} \quad (1)$$

where PSS_{mix} was proportional seed survival of species X in a seed patch with ORY and PSS_{single} was proportional seed survival of species X in a monospecific seed patch, where X represented each of the six species listed above. Likewise, a reciprocal indirect effect of X on ORY (i.e., $IS_{X \rightarrow ORY}$) was also determined (see *Measurement of indirect effects in the field*).

I expected a negative relationship between seed preference and $IS_{ORY \rightarrow X}$ (and $IS_{X \rightarrow ORY}$; Figure 1). Seeds that have a low

preference ranking should have little effect in attracting and retaining the rodents in the mixed-seed patches, hence predation on ORY should be about equal in the mixed and monospecific seed patches and predation on X should be negligible or nonexistent. That is, $IS_{ORY \rightarrow X}$ and $IS_{X \rightarrow ORY}$ should be near zero. Seeds that have a high preference ranking should attract and retain rodents in the mixed-seed patches thereby generating negative $IS_{ORY \rightarrow X}$ and $IS_{X \rightarrow ORY}$ values. In general, the strength of apparent competition (between the seeds of two species) should increase with increasing preference of seed predators for both seed species as long as one of the seed species is preferred relative to the other. This prediction assumes that the seed predators forage optimally; that is, they are selective density-dependent foragers.

I used an ordered-heterogeneity test (OH test) (Rice and Gaines, 1994a,b) to test for the expected pattern between seed preference and the strength of apparent competition. Ordered-heterogeneity tests are simultaneous tests of the differences among means and the expected order of means. The test that I used combined a one-way ANOVA with a Spearman rank-correlation test (Rice and Gaines, 1994a,b). The ANOVA tested for differences among the mean $IS_{X \rightarrow ORY}$ (or $IS_{ORY \rightarrow X}$) values while the Spearman rank correlation tested the predicted order of the mean $IS_{X \rightarrow ORY}$ or $IS_{ORY \rightarrow X}$ values (the predicted order was determined from preference rankings). The test statistic is the product of the Spearman rank correlation and the complement of the p value from the ANOVA, or $r_s(1 - p)$. Large values of this test-statistic indicate significance. Rice and Gaines (1994b) provide a table of critical values.

Measurement of indirect effects in the field

I obtained estimates of $IS_{X \rightarrow ORY}$ and $IS_{ORY \rightarrow X}$ under natural conditions by conducting a seed tray experiment at a study site in northern Nevada (for a detailed description of the study site see Breck and Jenkins, 1997; Jones and Longland, 1998; or Veech, 2000). Individuals of *D. merriami* and *P. longimembris* comprise 70–80% of the rodent community at the study site (Breck and Jenkins, 1997; Jones and Longland, 1998; Veech, 2000) so any indirect interactions between seed species observed in the field was probably due to one or both of these species. I established three blocks each of which consisted of four rows of 12 stations spaced 20 m apart. The rows were spaced at 80 m. I placed three small aluminum seed trays (diameter 22.5 cm, depth 5.5 cm) separated by 1 m at each station. The trays contained seeds of the following treatments buried under a 1 cm layer of sand: 100 seeds of ORY, 100 seeds of species X, or 100 seeds of ORY and 100 seeds of species X. At each station, species X represented one and only one of the following seed species: AST, LUP, PAN, PEN, SPH, and STA. Within each row, each species X was represented twice at randomly chosen stations for a total of eight per block. A total of three blocks yielded a sample size of 24 for each pairing of ORY with one of the species X. I paired each species with ORY (as opposed to some other species) because I knew a priori that heteromyid rodents have a strong preference for ORY seeds.

By burying the seeds I intentionally prevented the foraging of granivorous birds and ants. Trays were left out in the field for approximately 30 nights, after which I collected the trays and counted the number of seeds remaining in each tray. From these data, I determined $IS_{X \rightarrow ORY}$ and $IS_{ORY \rightarrow X}$ according to Equation 1. The seed tray experiment was conducted from 16 July 1998 to 13 August 1998 (Run 1) and again from 17 August 1998 to 19 September 1998 (Run 2).

Density-dependent foraging experiment

I examined the effect of seed density on the foraging behavior of 12 *D. merriami* individuals and five *P. longimembris* individ-

uals in mixed-species and monospecific seed patches. Each individual was allowed to forage by itself for 12 h in a large indoor arena ($4 \times 2 \times 1.5$ m) that contained five seed trays (22 cm diameter, 4.5 cm depth) and a sand substrate. These five trays represented the following treatments: (1) 200 ORY seeds, (2) 100 ORY seeds and 100 AST seeds (mixed tray), (3) 100 ORY seeds, (4) 200 AST seeds, and (5) 100 AST seeds. In a separate study (Veech JA and Jenkins SH, manuscript submitted) the apparent competition between ORY and AST was stronger than the apparent competition between ORY and any of the other species tested, so I chose ORY and AST for this experiment. I buried the seeds in each tray under a 2 cm layer of sand. I placed the trays midway between the nest-box at one end of the arena and the far wall at the other end. The trays were spaced about 0.75 m apart and treatment assignment to tray was randomized.

I placed each individual into the arena at hour 2000, 2 h after the start of the dark portion of the 12L:12D photoperiod, and removed it at 0800 the following day, 2 h after the start of the light portion of the photoperiod. I videotaped each individual and then scored the videotapes for the amount of time spent in each tray during a visit. To be considered a "visit" the rodent must have been in the tray digging through sand for at least 4 s. After each trial I collected and counted the number of ORY and AST seeds remaining in each tray. This allowed me to determine the harvest rate of each seed species.

The predicted order among treatments (for total time in tray as the response variable) depended on combined seed density of ORY and AST and on the separate single-species densities of ORY and AST. The predicted order among the three treatments that included ORY was tested separately from the predicted order among the three treatments that included AST. For ORY treatments the predicted order was 200-seed tray > mixed tray > 100-seed tray. Rodents should have spent the most time in the tray with the highest density of ORY seeds and the least time in the tray with the lowest overall density. Note that the mixed-species tray had a combined density of 200 seeds. For AST treatments the predicted order was mixed-species tray > 200-seed tray > 100-seed tray. Rodents should have spent the most amount of time in the mixed-species tray because it contained ORY seeds and the least amount of time in the tray with the lowest overall density. The two rodent species were tested separately. I tested the predicted order among treatments by using an ordered heterogeneity test (Rice and Gaines, 1994a,b) as previously described for the preference experiment.

I also tested for differences in rate of harvest of seeds from the different trays. Treatments containing ORY were tested separately from those containing AST and the two rodent species were tested separately. I did not make any predictions about the order of harvest rate among the treatments, because harvest rate could potentially increase or decrease as the total time spent in a tray increased. An increase in harvest rate could occur if rodents become more efficient at finding seeds with increasing time spent in a tray or it could decrease if the depletion of seeds causes rodents to spend more time finding the remaining seeds. So, the comparison among treatments was limited to testing for differences using a repeated measures ANOVA (rmANOVA).

RESULTS

Seed preference

Individuals of *D. merriami* exhibited strong preferences for ORY, PAN, and SPH. They had intermediate preferences for AST, BRO, and LUP, and generally avoided harvesting PEN and STA seeds (Figure 2). The two *P. longimembris* individuals

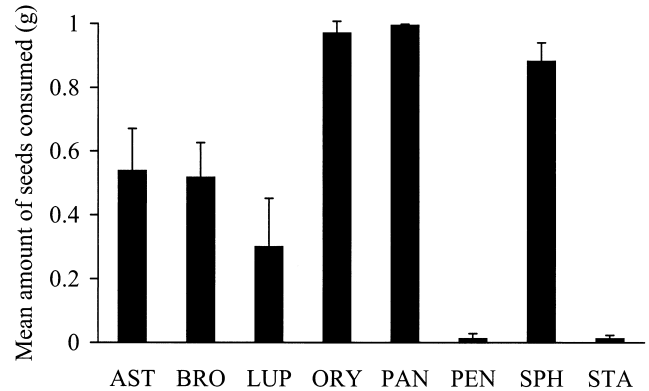


Figure 2

Mean preferences of *Dipodomys merriami* individuals for seeds of eight plant species. Preference is estimated as the amount (0–1 g) of seeds consumed. Error bars represent + 0.5 SD.

that were tested exhibited similar preferences except that they had lower preference for AST seeds than did *D. merriami*. Given that the rodents exhibited varying preferences for the different seeds, it was possible to examine the relationship between seed preference and the indirect interaction between seed species (IS values). Recall that both $IS_{X \rightarrow ORY}$ and $IS_{ORY \rightarrow X}$ were predicted to become more negative as preference for X increased (Figure 1). However, this inverse relationship was found to be significant only for the $IS_{X \rightarrow ORY}$ values obtained during Run 2 of the seed-tray experiment [$r_s(1 - p) = -0.913$, $p_{OH} < .001$, OH test; Figure 3D]. The IS values obtained during Run 1 of the experiment were probably too small to allow for a powerful test of the relationship between IS and seed preference (Figure 3A,C).

Density-dependent foraging experiment

In this experiment, rodents were tested for whether they exhibit density-dependent foraging for ORY seeds. The response variables were total amount of time spent in tray and rate of seed harvest. Rodents were expected to spend the most amount of time in the tray containing 200 ORY seeds followed by the mixed-seed tray (100 ORY, 100 AST), and the tray containing 100 ORY seeds. For *D. merriami* the difference in foraging time among the seed-tray treatments was not significant ($F = 0.48$, $df = 2,22$, $p = .623$, rmANOVA) and the order was not as predicted ($r_s(1 - p) = 0.141$, $p_{OH} = 0.375$, OH test; Figure 4A). The same was true for *P. longimembris*; there was only a marginally significant difference among treatments ($F = 3.95$, $df = 2,8$, $p = .064$, rmANOVA) and a lack of the predicted order ($r_s(1 - p) = 0.141$, $p_{OH} = 0.375$, OH test; Figure 4A).

I also tested for density-dependent foraging of AST seeds. Rodents were expected to spend the most amount of time in the mixed-seed tray because it contained the highly preferred ORY seeds in addition to AST seeds. The amount of time spent in the tray containing 200 AST seeds was expected to be greater than the amount of time spent in the tray containing 100 AST seeds based on the density difference alone. For *D. merriami* there were significant differences among the treatments containing AST seeds ($F = 6.53$, $df = 2,22$, $p = .006$, rmANOVA). *D. merriami* individuals appeared to spend time in the trays in the predicted order ($r_s(1 - p) = 0.562$, $p_{OH} < 0.1$, OH test) though this finding is only marginally significant (Figure 5A). Individuals of *P. longimembris* also spent significantly different amounts of time foraging in the trays of each treatment ($F = 13.87$, $df = 2,8$, $p = .003$, rmANOVA) although the treatments were not in the predicted order (Figure 5A).

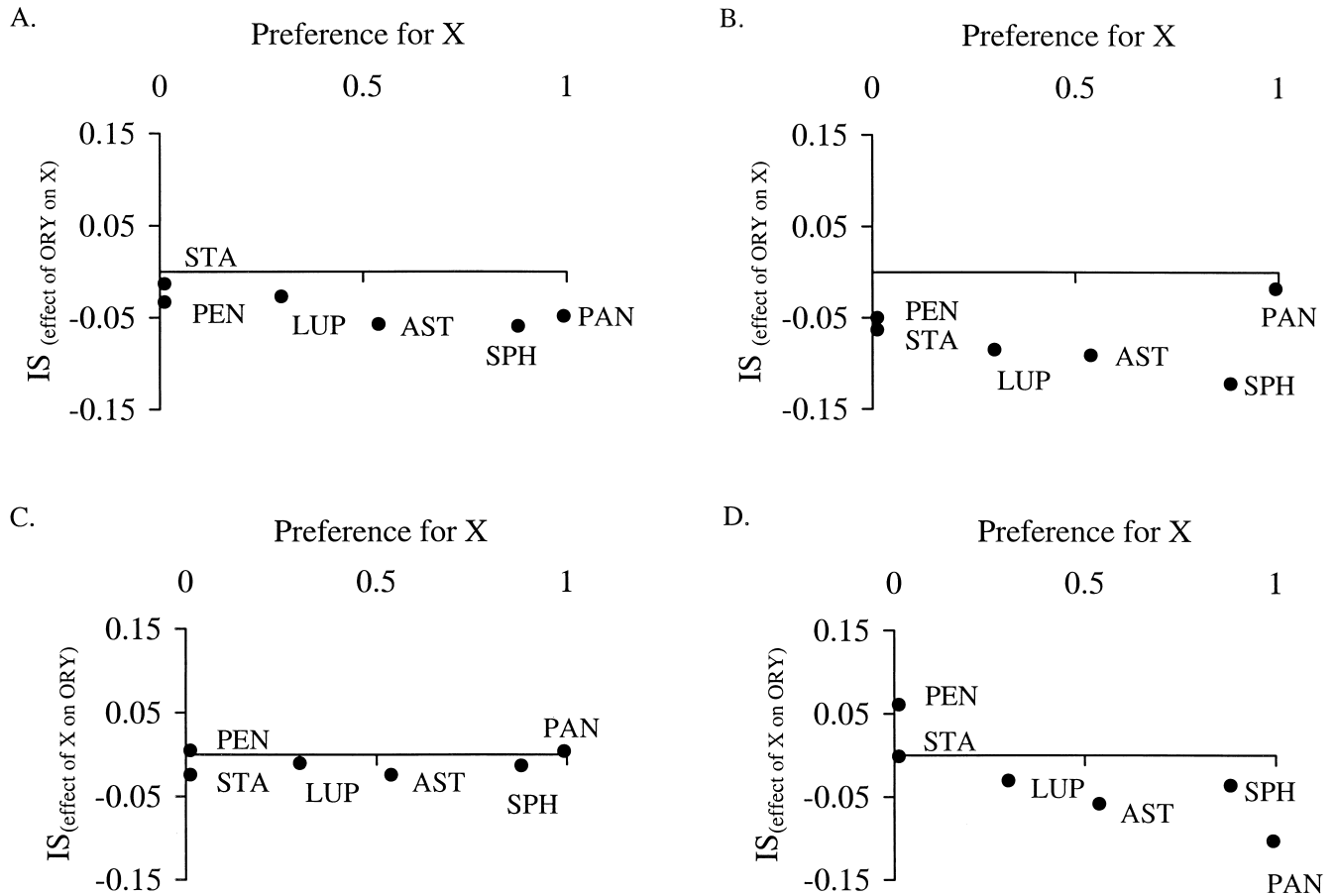


Figure 3

The relationship between preference for seeds of species X and the indirect effect of ORY on survival of X ($IS_{ORY \rightarrow X}$) for IS values obtained from (A) Run 1 and (B) Run 2 of the seed-tray experiment designed to detect such indirect effects. The relationship between preference for X and the indirect effect of X on ORY ($IS_{X \rightarrow ORY}$) is also shown for (C) Run 1 and (D) Run 2. The predicted inverse relationship between seed preference and the strength of apparent competition (measured by IS) was found to be significant only for $IS_{X \rightarrow ORY}$ during Run 2. The same results were obtained whether preference was measured as absolute consumption of seeds in grams (as shown) or relative consumption (not shown).

Recall that I did not predict the order of harvest rate (i.e., total number of seeds harvested divided by total amount of time in a tray) in the different seed-tray treatments. However it was important to measure harvest rate because differences in harvest rate might explain the existence of short-term apparent competition if there is no difference in the amount of time rodents spend in the different trays. Harvest rate of ORY seeds by *D. merriami* individuals was significantly different among the trays ($F = 3.85$, $df = 2,22$, $p = .037$, rmANOVA) as was harvest by *P. longimembris* individuals ($F = 6.03$, $df = 2,8$, $p = .025$, rmANOVA; Figure 4B). Because *P. longimembris* individuals did not harvest any AST seeds, comparison of the harvest rate of AST was limited to *D. merriami*. Harvest rate of AST was significantly different among the trays ($F = 24.02$, $df = 2,22$, $p < .0001$, rmANOVA; Figure 5B). The rodents harvested seeds from the 200-seed AST treatment at a much faster rate than from other treatments (200-seed tray versus mixed-seed tray, $p < .0001$; 200-seed tray versus 100-seed tray, $p < .0001$; Bonferroni posthoc pairwise comparisons; Figure 5B).

DISCUSSION

Behavioral causes of short-term apparent competition

Under natural conditions heteromyid rodents can induce short-term apparent competition between the seeds of differ-

ent plant species (Veech, 2000; Veech JA and Jenkins SH, manuscript submitted). In addition, heteromyids definitely prefer some seeds to others. However, in contrast to the prediction, seed preference appears to have only an occasional effect on the strength of short-term apparent competition between seeds. The expected inverse relationship between seed preference and the indirect effect of one seed species on another was found in only one of four repetitions of the seed-tray experiment. Likewise, density-dependent foraging effort does not fully explain the existence of apparent competition. The results of the density-dependent foraging experiment indicate that rodents did not spend an increased amount of time in the mixed-species trays as compared to the trays containing just *O. hymenoides* seeds. Individuals of *D. merriami* and *P. longimembris* spent approximately equal amounts of time in the seed trays containing a high density of *O. hymenoides* seeds and those containing a low density of *O. hymenoides* seeds and less time in trays which contained *O. hymenoides* seeds mixed with seeds of *Astragalus cicer* (AST, Figure 4A). Foraging effort, defined as the amount of time spent foraging, was not dependent on the initial density of seeds in a tray. Assuming these results can be extrapolated to the foraging behavior of rodents in a natural setting, the short-term apparent competition documented in the seed-tray experiment may have been due to some cause other than density-dependent foraging effort.

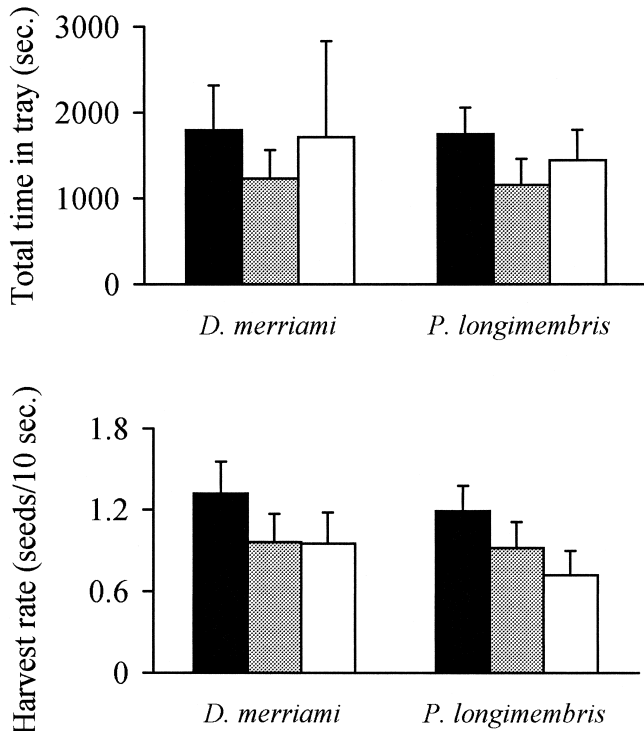


Figure 4
Results of the density-dependent foraging experiment for *Dipodomys merriami* individuals ($N = 12$) and *Perognathus longimembris* individuals ($N = 5$) foraging in trays representing the following treatments: 200-seed ORY, black bar; mixed seed, gray bar; and 100-seed ORY, white bar. Bars depict means for each species. Note that bars are in the predicted order of treatment means for (A) the total amount of time spent in trays of each treatment and (B) harvest rate. Error bars represent + 0.5 SD. ORY, *Oryzopsis hymenoides*.

Given that seed preference and density-dependent foraging do not completely explain the existence of apparent competition among seeds, what other aspect of rodent foraging behavior does? Despite the fact that heteromyid rodents have distinct seed preferences, they are known to harvest the seeds of a wide variety of plant species (Henderson, 1990; Reichman, 1975, 1977). This suggests that prey-switching behavior may be a cause of short-term apparent competition. In this scenario, a rodent enters a seed patch and forages exclusively for the seeds of the preferred species. As these seeds are depleted the rodent switches prey and begins foraging for the seeds of the less-preferred species. This prey-searching behavior allows the rodent to remain in the patch for an increased amount of time. This, thus, leads to a greater amount of predation on the seeds of both species in the mixed-species seed patch than in the single-species seed patch. This scenario should sound familiar; it is the same one presented in the Introduction to explain the effect that a highly preferred seed species has on attracting and retaining rodents. The difference, here, is that the propensity for a rodent to switch prey, regardless of preference, results in the rodents spending more time in the mixed-species seed patches but that extra time does not depend on which prey the rodent switches to. Hence, the relationship between seed preference and indirect interaction strength (Figure 1) is weak or nonexistent. Such prey-switching behavior would explain why seed-tray experiments can uncover short-term apparent competition in the field that does not seem to be influenced by seed preference in the laboratory.

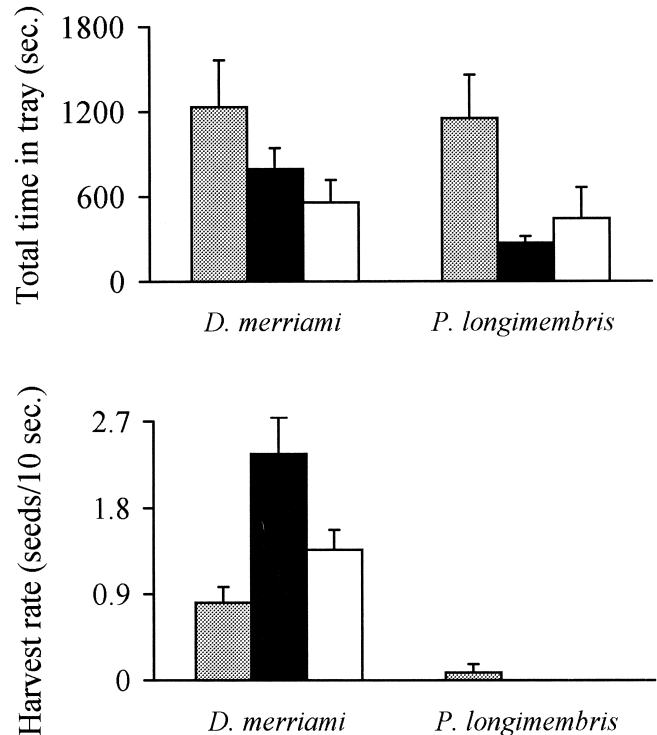


Figure 5
Results of the density-dependent foraging experiment for *Dipodomys merriami* individuals ($N = 12$) and *Perognathus longimembris* individuals ($N = 5$) foraging in trays representing the following treatments: 200-seed AST, black bar; mixed seed, gray bar; and 100-seed AST, white bar. Bars depict means for each species. Note that bars are in the predicted order of treatment means for (A) the total amount of time spent in trays of each treatment and (B) harvest rate. Individuals of *P. longimembris* did not harvest any AST seeds from the trays containing only AST seeds. Error bars represent + 0.5 SD. AST, *Astragalus cicer*.

Prey-switching behavior enables a predator to maintain a greater instantaneous rate of prey capture than it would have if it did not switch prey. However, even without prey-switching, an increase in the instantaneous harvest rate of prey in a mixed-species patch can cause short-term apparent competition. The predator may forage for both prey simultaneously throughout the entire foraging bout such that a "switch" never occurs. For instance, a decrease in the survival of seeds in mixed-species patches can arise from a rodent increasing its instantaneous harvest rate of one or both species in mixed-species patches compared to the harvest rate in single-species patches. In such a scenario the amount of time spent in the mixed-species and single-species patches could be relatively equal (i.e., no density-dependent foraging effort or preference effect) and yet short-term apparent competition still could be caused by the foraging behavior of a rodent.

On the other hand, apparent competition can also arise when foraging effort is greater in the mixed-species patches even if the harvest rate is lower in the mixed-species patches than in the single-species patches. Individuals of *D. merriami* harvested *A. cicer* seeds at a lower rate in the mixed-species patches compared to the monospecific low density patches of *A. cicer*, but because they spent more time in the mixed-species patches they induced a negative indirect effect ($IS_{ORY \rightarrow AST} = -0.153$) of *O. hymenoides* on survival of *A. cicer* seeds at low density (Table 1). As might be expected, an apparent mutualism can arise when the harvest rate is greater in the single-species patches than the mixed-species patches, regardless of

Table 1

The indirect effect of ORY on survival of AST seeds ($IS_{ORY \rightarrow AST}$) and the reciprocal indirect effect of AST on survival of ORY seeds ($IS_{AST \rightarrow ORY}$) for comparisons of seed survival in mixed-species seed trays versus survival in either high or low density monospecific trays of the density-dependent foraging experiment

Rodent species	Comparison	$IS_{ORY \rightarrow AST}$	$IS_{AST \rightarrow ORY}$
Dipodomys merriami ($N = 12$)	Mixed versus high density	0.158	0.020
Perognathus longimembris ($N = 5$)	No harvest	No harvest	0.068
D. merriami ($N = 12$)	Mixed versus low density	-0.153	-0.006
P. longimembris ($N = 5$)	No harvest	No harvest	-0.030

Individuals of *Perognathus longimembris* did not harvest any AST seeds from the monospecific trays thus precluding determination of $IS_{ORY \rightarrow AST}$. AST, *Astragalus cicer*; ORY, *Oryzopsis hymenoides*.

foraging effort. *D. merriami* individuals spent more time in the mixed-species patches than in the monospecific high density patches of *A. cicer*, but because their harvest rates were greater in the latter type of patch they induced a positive indirect effect ($IS_{ORY \rightarrow AST} = 0.158$) of *O. hymenoides* on survival of *A. cicer* seeds at high density. The results of this study demonstrate that there is no single behavior of heteromyid rodents that can account for the existence of short-term apparent competition among seeds.

Optimal foraging and apparent competition

Based on a theoretical consideration of optimal diet choice Holt and Kotler (1987) predicted that optimal foraging could lead to short-term apparent competition under some conditions. Foraging is optimal when a predator reduces prey to the same giving-up density in all patches (Charnov, 1976). Whether this reduction involves prey-switching depends on the average density of both prey in the environment. According to the marginal value theorem (Charnov, 1976) a predator should cease foraging in a patch when its instantaneous rate of prey harvest equals the rate it could obtain elsewhere (i.e., the average rate throughout the environment). Therefore, a predator foraging optimally in a prey-rich environment should leave a patch before switching to a less-preferred prey. But, an optimally foraging predator in a prey-deficient environment should switch to the less-preferred prey before leaving a patch (Holt and Kotler, 1987). Based on the lack of a strong relationship between seed preference and indirect interaction strength, I indirectly inferred that rodents switch prey during a foraging bout but that the extra time gained by the switch is relatively constant and does not depend on preference for the second prey. I assume that the seed trays used in the seed-tray experiment represented high-density prey patches in a generally prey-deficient environment (background seed densities at the study site are low; unpublished data). This suggests that heteromyid rodents at the study site forage optimally, first selectively then opportunistically, in their choice of prey. This type of prey-switching behavior can lead to short-term apparent competition between the prey (Brown and Mitchell, 1989; Holt and Kotler, 1987) but the results of this study suggest that it does not influence the actual strength of that short-term apparent competition.

Switching to less preferred prey may occur if there is an increase in the search time (i.e., decrease in encounter rate) necessary for obtaining an item of the preferred prey (Krebs et al., 1977). That is, a forager may switch prey when its rate of encountering preferred prey has become too low and not necessarily because it has yet to reduce prey density to the average environmental density. If the predator has not sampled patches then it does not have an estimate of environmental prey density anyway. Prey-switching within a patch is also more likely to occur if the cost of moving among patches

is high. The marginal value theorem (Charnov, 1976) includes the cost of moving among patches. That is, the average rate of prey yield throughout the environment includes the cost (or time) that accrues when a predator must move among patches. Therefore, if the cost of moving among patches is high then the average rate of prey yield is low. When the environment-wide average rate of prey yield is low, a predator should decrease prey density to a lower giving-up density than it would have otherwise. Alternatively, the predator may not forage in accord with the marginal value theorem but simply remain longer in a patch if travel costs are high. Regardless the extra time spent in a patch can lead to prey-switching and short-term apparent competition. However, relative prey preferences should have little effect on the strength of short-term apparent competition when travel costs are high enough that a predator will switch to a less-preferred prey (including the least favored prey) rather than incur the cost of traveling to another patch. The lack of a relationship between seed preference and indirect interaction strength might be explained by the cost that heteromyid rodents accrue when they move among seed patches. This combination of diet choice (i.e., prey preference within a patch) and patch choice (i.e., patch use as a function of travel cost) deserves further attention by ecologists interested in short-term apparent competition.

For a given seed species, the captive rodents had about the same foraging effort in the high and low density monospecific seed patches of the density-dependent foraging experiment. An optimal use of patches predicts that foraging effort should be greater in the patch with a higher prey density assuming the predator has sampled patches and knows which has the higher prey density (Lewis, 1980; McNair, 1982). Perhaps, the rodents did not utilize the high-density seed patches significantly more than the low-density seed patches because their functional responses (i.e., rates of seed harvest) were plastic. The same giving-up density of seeds could be obtained with the same foraging effort in patches with both high and low seed densities. Because giving-up density was equalized in high and low density seed patches the captive rodents appear to have foraged optimally within the experimental arena. This resulted in either short-term apparent competition or a positive indirect interaction (Table 1). Therefore, a predator foraging optimally does not always induce short-term apparent competition.

Conclusion

Short-term apparent competition among prey species is always caused by the behavior of individual predators. Predators must actively search for and capture prey. However, searching for and capturing prey is not sufficient for causing short-term apparent competition. Short-term apparent competition exists when the capture of a given prey species is greater due to the presence of another prey species. That is, the behavior of the

predator is altered when it is searching for both prey as opposed to only one prey, or when it is searching for a given prey in an area where it will also encounter another type of prey. For instance, *D. merriami* individuals harvested a greater proportion of *A. cicer* seeds in patches that also contained seeds of *O. hymenoides* than in patches that did not, because they spent more time foraging in the patches that contained *O. hymenoides* seeds than in the patches that did not. Holt and Kotler (1987) reasoned that the presence of an alternative prey within a patch could permit predators to remain in the patch longer, before capture rates become suboptimal, such that the increased time would result in an increased proportion of either one or both prey being captured, hence apparent competition. The foraging behavior of captive *D. merriami* individuals supported this prediction of short-term apparent competition but their presumed behavior in the field did not predict the strength of the apparent competition.

Establishing causal links between the behavior of individual organisms and community structure is not easy. However, much theory (e.g., optimal foraging theory) already exists to help ecologists and behaviorists establish these links. Holt and Kotler (1987) derived the theoretical expectation of short-term apparent competition from optimal foraging theory and thereby provided a theoretical example of how the behavior of individual organisms could affect the distribution and abundance of other organisms, particularly prey species. Since then other researchers (Chaneton and Bonsall, 2000; Menge, 1997) have uncovered evidence that apparent competition (short-term and long-term) may be relatively common. To my knowledge, the present study is the first to both document short-term apparent competition and test whether its existence is due to a specific, observable behavior of the predator. Future behavioral studies should be able to document additional instances of species interactions caused by the behavior of individual animals. Ideally, these studies will investigate behavior in more detail than does the present study. Researchers should examine the prey-searching behavior of predators as well as prey capture behavior and the great variety of behavior that results from an individual having conflicting demands on its time and energy. Variation in the strength and direction of indirect effects between species may be rooted in the variable behavior of individuals, thus necessitating a comprehensive study of behavioral repertoires and not just a single behavior. Given that much of an individual's behavior is often adaptive, the distribution and abundance of species (i.e., community structure) might ultimately be explained by the evolutionary processes that mold behavior.

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