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## Predator-mediated interactions among the seeds of desert plants

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**Abstract** In theory, seed predators are capable of inducing indirect interactions among the seeds they consume. However, empirical evidence of predator-mediated interactions among seeds is rare. Rodents in the Heteromyidae are highly granivorous and therefore likely to induce indirect interactions among the seeds of desert plants. The indirect interactions may be in the form of apparent competition and apparent mutualism between seeds within a patch. Apparent competition exists when the survival of seeds of a focal species is lessened because of the presence of additional seeds of other species in the patch. Apparent mutualism exists when the presence of the other seeds results in an increase in survival of seeds of the focal species. By measuring seed removal from trays placed in the field, apparent competition between the seeds of several plant species was detected. Apparent mutualism might also exist, but there was no strong evidence of it. Apparent competition appeared most likely to occur among the species whose seeds were the most heavily predated. For instance, predation on seeds of *Astragalus cicer*, *Oryzopsis hymenoides*, and *Sphaeralcea coccinea* was substantial with more than 50% of the seeds removed from the trays, on average. The intensity of apparent competition (measured by the indirect effect, IS) between these species and two others was significant; IS ranged from  $-0.02$  to  $-0.39$  on a scale of 0 to  $-1$ . This indicates that, in some communities, indirect effects are most likely to exist when direct effects are strong.

**Key words** Indirect effects · Apparent competition · Seed predation · Heteromyid rodents

### Introduction

Granivorous rodents of the family Heteromyidae are widespread in the desert regions of North America. They disperse, cache, and consume the seeds of many species of desert plants (Reynolds 1950; McAdoo et al. 1983; McAuliffe 1990; Longland 1995). These activities may influence the structure of plant communities by affecting relative recruitment success (Longland 1995). Granivorous rodents can alter the composition of seed banks by selectively harvesting some seed types and ignoring others (Reichman 1976; Nelson and Chew 1977; Brown et al. 1979; Inouye et al. 1980; Henderson et al. 1988; Brown and Heske 1990; Samson et al. 1992; Price and Joyner 1997). Because of this selective predation, granivorous rodents probably induce indirect interactions among seed-producing plant species. In such a scenario, the interaction between species occurs at the seed stage of the life cycle, not at the plant stage as would be the case for a herbivore inducing apparent competition between growing plants, direct competition between seeds is very unlikely. Hence, the only types of interactions possible between seeds are apparent competition and apparent mutualism.

Predator-mediated interactions are often classified as either apparent competition or apparent mutualism. Apparent competition occurs when an increase in the abundance of one species leads to a decrease in the abundance of a second species, and apparent mutualism occurs when an increase in the first leads to an increase in the second (Holt 1984; Holt and Kotler 1987; Abrams and Matsuda 1996). However the change in abundance (increase or decrease) is actually due to a third species, such as a seed predator. The presence of a highly preferred seed type at high density may lead to functional, aggregative, or numerical responses in the populations of seed predators. If a seed patch consists of additional seed types as well as the preferred seed type then either of the three responses above may lead to decreases in the abundances of all seed types. These simultaneous decreases

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then appear to be competitive, hence the label “apparent competition”. On the other hand if the density of the preferred seed type is high enough then the seed predators may switch to it or become satiated on it so that the *relative* abundances of the other seed types increase and they appear to benefit from the presence of the highly preferred seeds, hence the label “apparent mutualism”. Just as with apparent competition, apparent mutualism can also be induced through functional, aggregative, or numerical responses by the predators to the presence of seed patches that differ in density of the preferred seed type. For instance, predators may be more attracted to and spend more time foraging in patches with a high density of the preferred seed type such that patches with a lower density are ignored. If the low-density patches contain other seed types as well, then the higher survival of the preferred seed type in these patches may appear to be mutualistic.

Brown and Mitchell (1989) reasoned that the behavior of a foraging rodent could generate a negative interaction between seed species. They found that increasing the density of either husked or unhusked millet in a patch increased the harvest of the other. Following Holt and Kotler (1987) they labeled this interaction “short-term apparent competition”. However, Brown and Mitchell (1989) used non-native seeds; until now, no one has tested the hypothesis that seed predators can induce indirect interactions among the seeds of naturally occurring plants.

My goal in this study was to test for apparent competition and apparent mutualism among the seeds of the following species of plants: *Oryzopsis hymenoides*, *Astragalus cicer*, an unidentified *Penstemon* sp., *Sphaeralcea coccinea*, and *Stanleya pinnata*. I also measured the negative direct effect of seed predation on each of the five species of seeds. Because heteromyid rodents usually prefer to forage for large seeds (Price and Podolsky 1989; Henderson 1990; Podolsky and Price 1990), particularly seeds of *O. hymenoides* (Johnson and Jorgensen 1981; McAdoo et al. 1983; Kelrick et al. 1986; Henderson 1990), I expected that the negative direct effect of predation would be greatest on *O. hymenoides*. But, beyond that hypothesis and the simple hypothesis that indirect interactions do exist among the five seed types I was unable to propose any specific hypotheses about the intensity or direction of the indirect interactions. As will be explained later, the direction and magnitude of the indirect interactions are restricted by the intensity of predation on each species.

## Methods

### Study site and species

The study was conducted in northwestern Nevada in an area known as Nightingale Flat (39°50'30"N, 119°00'10"W) which is about 80 km northeast of Reno, Nevada, United States. The vegetation of the area is typical of the shadscale-dominated desert of the Great Basin. In addition to shadscale (*Atriplex confertifolia*),

other shrubs such as greasewood (*Sarcobatus baileyi*), horsebrush (*Tetradymia spinosa*), and burrobush (*Hymenoclea salsola*) are abundant. The area between shrubs is dominated by cheatgrass (*Bromus tectorum*), Indian ricegrass (*Oryzopsis hymenoides*), and in occasional years, cicer milkvetch (*Astragalus lentiginosus*). Of the five plant species included in this study, two (*O. hymenoides* and *Sphaeralcea coccinea*) grow on the study grid, two (an unidentified *Penstemon* sp. and *Stanleya pinnata*) can be found growing within 1 km of the grid, and one (*Astragalus cicer*) does not grow at the study site. Seeds of *A. cicer* were intended to be a substitute for *A. lentiginosus* because I could not obtain seeds of the latter; the two species have approximately equal seed masses. I chose these species because of their relatively large seed masses (large seed mass is a good indicator that rodents will harvest the seeds) and because these plants were locally abundant (except *A. cicer*). Seed mass of each species was determined by obtaining the weight of 30 25-seed portions of each species, calculating the mean, and then dividing by 25 to get individual mean seed mass. I obtained the following individual mean seed masses for each species: *A. cicer*, 3.84 mg; *O. hymenoides*, 4.13 mg; *Penstemon* sp., 1.05 mg; *Sp. coccinea*, 1.50 mg; and *St. pinnata*, 1.53 mg. I collected seeds of *Penstemon* sp., *Sp. coccinea*, and *St. pinnata* from plants growing at the study site. Seeds of *O. hymenoides* and *A. cicer* were purchased from the Granite Seed Company, Lehi, Utah, United States. The following species of heteromyid rodents have been trapped at Nightingale Flat: *Dipodomys deserti*, *D. microps*, *D. merriami*, *Microdipodops megacephalus*, *Chaetodipus formosus*, *Perognathus longimembris*, and *P. parvus* (Breck and Jenkins 1997; Jones and Longland 1999). Trapping for rodents on the study grid on 21 June 1998 verified the presence of all of these species except *D. deserti* and *C. formosus*. The heteromyid community on the study grid is very diverse but is dominated numerically by *D. merriami*, which accounted for 70% of all individuals captured.

### Experimental design and analysis

I designed a field experiment for detecting an indirect effect of a group of four seed species on a single seed species. A permanent grid of 40 stations was established at the study site. I placed 10 stations at 20 m intervals, along each of four transects spaced 80 m apart, for a total of 40 stations. At each station I placed six seed trays of either a high-density ( $n=20$  stations) or low-density treatment ( $n=20$  stations). The high-density treatment consisted of the following layout: five trays each of which contained 125 seeds of a single species and a sixth tray containing 25 seeds each of all five species. The low-density treatment was identical except each single-species tray contained only 25 seeds. These numbers of seeds represented realistic seed densities within naturally occurring patches. The plant species used in this study are prolific seed producers; a single individual is capable of producing up to 1,000 or more seeds over the course of a month. All five species produce and release seeds during the summer, so patches containing all five species as well as patches containing only one species probably occur at the study site. The former may exist where individuals of each plant species exist in close proximity; e.g., within a square meter. The latter may exist directly under or adjacent to an individual plant in relative isolation from other plants. The two density treatments alternated between stations on a transect. The six trays at each station were arranged in either a complete circle or arc such that there was about 1 m between adjacent trays. This layout was intended to ensure that each tray at a station had an equal probability of being detected by a foraging rodent.

The circular aluminum trays (22 cm diameter, 4.5 cm depth) were filled to a depth of 1 cm with locally obtained sand that had been cleaned and sifted to remove seeds and large debris. Then I sprinkled the seeds on the trays and covered the seeds with a 0.5-cm layer of sand. Burying the seeds in this way simulated the seed bank and prevented avian predation on the seeds; although avian seed predators were infrequent at the study site during the summer. Ant predation on the seeds was prevented because ants were

unable to climb into the trays. The seed trays were left out in the field for six consecutive nights. This was intended to be sufficient time for rodents to find and forage in the trays if they so chose. I then sorted and counted the seeds remaining in each tray. This experiment was conducted from 2 August 1997 to 8 August 1997 and then repeated from 7 September 1997 to 13 September 1997.

The proportion of seeds remaining in each tray was determined. From that, I calculated the strength of the indirect effect (IS) of the four-species community on each of the five species as

$$IS = PSS_{\text{mix}} - PSS_{\text{single}} \quad (1)$$

where  $PSS_{\text{mix}}$  is proportionate seed survival of species  $X$  in the mixed-species tray and  $PSS_{\text{single}}$  is proportionate seed survival of species  $X$  in the single-species tray, for  $X$ =each of the five species studied. For instance, if  $X$  was *A. cicer*, then the four-species community consisted of *O. hymenoides*, *Penstemon* sp., *Sp. coccinea*, and *St. pinnata*. A positive value of IS is produced when rodents harvest a greater proportion of seeds from the single-species tray than from the mixed-species tray. If the harvesting pattern is the opposite of this then a negative IS value is produced. A positive IS value indicates apparent mutualism and a negative value indicates apparent competition. This method of calculating indirect effects is similar to that employed by Miller (1994).

For each of the 40 stations I obtained the strengths of the indirect effects (IS values) and the strengths of the direct effects (DE values) of seed predation on each of the five species. For each species, DE is defined as the number of seeds removed from the mixed-species tray ( $N_{\text{mix}}$ ) and the single-species tray ( $N_{\text{single}}$ ) expressed as a proportion of the total number of seeds in both trays:

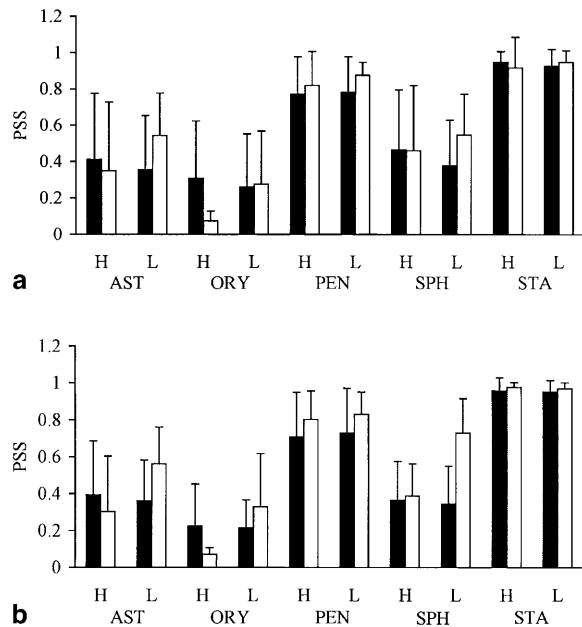
$$DE = [(1 - PSS_{\text{mix}}) \times N_{\text{mix}} + (1 - PSS_{\text{single}}) \times N_{\text{single}}] / (N_{\text{mix}} + N_{\text{single}}) \quad (2)$$

Prior to analyzing the data, the interaction strengths (which were proportions) were arcsine-transformed in an attempt to obtain normal distributions of the variable (Sokal and Rohlf 1995). However, one-sample Kolmogorov-Smirnov tests indicated non-normality in the distributions. Therefore, I used a randomization test to determine whether the strengths of the indirect effects (IS values) were significantly different from zero (Appendix 1).

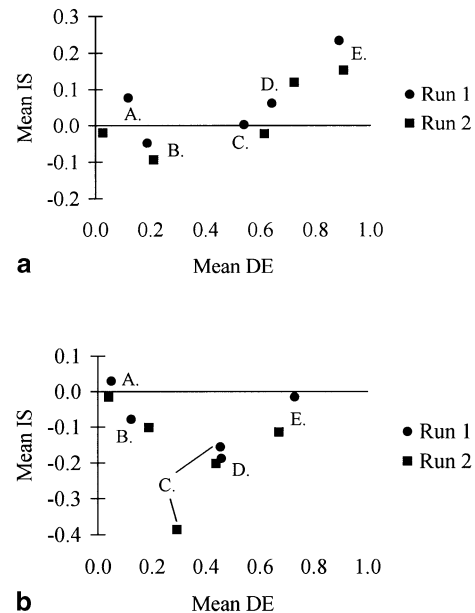
## Results

Proportionate seed survival ranged from less than 0.10 (*O. hymenoides* at high density) to over 0.9 (*St. pinnata*) (Fig. 1a,b). For all species except *St. pinnata*, PSS was generally greater in the low-density monospecific trays than the high-density monospecific trays (Fig. 1). PSS was also very consistent within each species over the course of both runs of the experiment.

There were significant negative indirect effects of the four-species community on survival of seeds of *A. cicer* (low-density treatment, runs 1 and 2), *O. hymenoides* (low-density treatment, runs 1 and 2), and *Sp. coccinea* (high and low-density treatments, run 2) (Table 1). In other words, survival of *A. cicer* and *Sp. coccinea* seeds was greater when those seeds occurred at low density in monospecific seed patches (trays) than when they were mixed with the other four species. Two species, *Penstemon* sp. and *St. pinnata*, had no significant IS values. That is, the slightly negative indirect effect of the four-species community on each species was not statistically significant, although the indirect effect on *Penstemon* sp. was almost significant at low density (IS=-0.078, run 1; IS=-0.101, run 2) (Table 1). The indirect effect on *St. pinnata* was always near zero (-0.02 < IS < 0.03).



**Fig. 1** Mean proportionate seed survival (PSS) for each species in both mixed-species trays (filled bars) and single-species trays (open bars) at both high (H) and low (L) densities for **a** run 1 and **b** run 2 of the seed-tray experiment (AST *Astragalus cicer*, ORY *Oryzopsis hymenoides*, PEN *Penstemon* sp., SPH *Sphaeralcea coccinea*, STA *Stanleya pinnata*). Error bars represent +1 SD



**Fig. 2** The mean strength of the indirect effect (IS) of the four-species community on each of the five species and the strength of the direct effect of seed predation (DE) on each of the five species for **a** the high seed density treatment and **b** the low seed density treatment (A. *Stanleya pinnata*, B. *Penstemon* sp., C. *Sphaeralcea coccinea*, D. *Astragalus cicer*, E. *Oryzopsis hymenoides*)

**Table 1** Results of the randomization test. The test determines whether the indirect effect (IS) of the four-species communities on each of the five species is statistically significant. Results of the tests are presented as the proportion of 1,000 iterations that gave an IS value greater than (either more positive or more negative) than the observed IS value. IS values with proportions less than 0.05 are considered statistically significant (*DE* direct effect of predation)

Species	Run	Density treatment	Mean DE	Mean IS	Randomization test
<i>Astragalus cicer</i>	1	High	0.642	0.062	0.998
	2	High	0.723	0.119	0.987
	1	Low	0.458	-0.188	0.018
	2	Low	0.438	-0.202	0.022
<i>Oryzopsis hymenoides</i>	1	High	0.887	0.234	0.331
	2	High	0.903	0.152	0.939
	1	Low	0.731	-0.015	0.039
	2	Low	0.672	-0.114	0.045
<i>Penstemon</i> sp.	1	High	0.188	-0.048	0.985
	2	High	0.212	-0.094	0.958
	1	Low	0.124	-0.078	0.053
	2	Low	0.189	-0.101	0.061
<i>Sphaeralcea coccinea</i>	1	High	0.541	0.003	0.993
	2	High	0.615	-0.022	0.006
	1	Low	0.455	-0.156	0.063
	2	Low	0.292	-0.386	0
<i>Stanleya pinnata</i>	1	High	0.044	-0.013	1
	2	High	0.027	-0.020	0.998
	1	Low	0.050	0.030	0.118
	2	Low	0.040	-0.016	0.130

Overall, the results were consistent between both runs of the experiment; i.e., significant results from both runs coincided (Table 1). In addition, for all five species the relationship between the indirect effects (as measured by IS) and the direct effects of predation (as measured by DE) was remarkably similar between both runs of the experiment (Fig. 2).

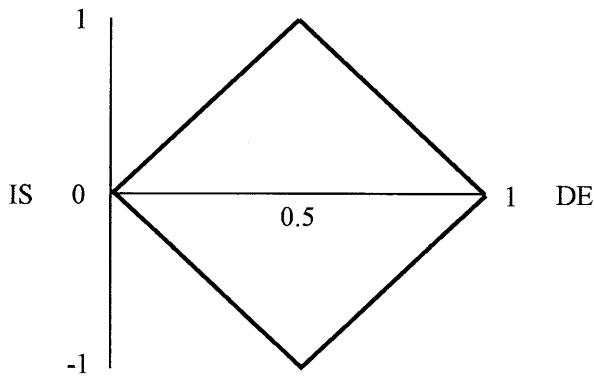
## Discussion

Through their predation on seeds, heteromyid rodents at the study site induced consistent indirect interactions among some of the seed-producing plant species. However, the plant species involved in these predator-mediated interactions were not a random subset of the five plant species tested. In particular, the three species, *A. cicer*, *O. hymenoides*, and *Sp. coccinea*, that were involved in indirect interactions with the other species also experienced the greatest predation intensity.

The lack of an indirect effect on *Penstemon* sp. and *St. pinnata* may be explained by a lack of substantial predation on those two species. Recall that the indirect effect (IS) is defined as the proportion of seeds surviving in the mixed-species tray minus the proportion of seeds surviving in the single-species tray (Eq. 1). The direct effect (DE) is defined as the average proportion of seeds removed from the single-species tray and the mixed-species tray (Eq. 2). The range of possible IS values is restricted by DE, the maximum range of -1 to 1 can only occur when DE=0.5. Furthermore, when DE is very high or very low, IS is severely restricted (Fig. 3). This may partially explain why the *Penstemon* sp. and *St. pinnata* were not involved in any indirect interactions; there was simply not enough predation on those species.

The only plant species (*O. hymenoides*) that appeared to significantly benefit by being in the presence of the other four species had the largest seeds and the most preferred seeds as measured by predation intensity (DE). But, the benefit that *O. hymenoides* received from the other four species only occurred when seed survival in the mixed-species trays was compared to survival in the single-species trays at high density and this positive indirect effect was not statistically significant (Table 1). Even though the indirect effect was not significant, the greater survival of *O. hymenoides* seeds in the mixed-species trays than in the high-density single-species trays suggests that rodents may have been attracted to those monospecific seed patches more often or may have spent more time foraging in those patches than in the mixed-species seed patches.

In the Introduction, I described how functional and aggregative responses to the presence of a highly preferred seed type in a mixed-seed patch could lead to apparent competition because less preferred seeds are also consumed when a predator is attracted to a mixed-seed patch. The lower survival of *A. cicer* and *Sp. coccinea* in mixed-seed patches compared to monospecific seed patches (at low seed density) may have been due to either a functional or aggregative response. That is, mixed-seed patches, containing highly preferred seeds (e.g., *O. hymenoides*), may have attracted seed predators more often or those predators may have spent more time foraging in those patches than in monospecific patches with a low density of seeds. When the monospecific patches contained a high density of seeds (125 per tray) the IS values were either near zero (*Sp. coccinea*) or positive and nonsignificant (*A. cicer*) (Fig. 2). This indicates that a high density of less preferred seeds in a monospecific patch negates the apparent competition that would other-



**Fig. 3** The relationship between the strength of the indirect effect (*IS*) and the negative direct effect of predation (*DE*) on survival of seeds. For a given value of *DE*, the *IS* value must lie within the diamond-shaped area. The range of possible *IS* values is maximized when  $DE=0.5$  and minimized as *DE* approaches 0 and 1, for cases in which the number of seeds in the mixed-species tray equals the number of seeds in the single-species tray. Otherwise the range of *IS* values is maximized at a *DE* value either less than or greater than 0.5, and the diamond shape is skewed either left or right

wise exist if the density were lower. In other words, rodents are attracted to and forage in monospecific seed patches with a high density of seeds even though those seed patches do not contain the preferred species.

The importance of predator behavior in mediating indirect interactions has been previously noted. Holt and Kotler (1987) suggested that the empirical study of species interactions and the development of theory could be advanced by focusing on the role of behavior in direct effects of one species on another and the indirect effects among species. In this study I found significant and consistent indirect interactions mediated by seed predators. This led to proposed explanations of the interactions that explicitly involved the behavior of the seed predators (e.g., the attraction of rodents to patches containing a high density of seeds). Although these explanations were not tested, they lend themselves to precise predictions that can be easily tested.

Future development and testing of theory concerned with indirect interactions mediated by predators might also profit from explicit analysis of the relationship between predation intensity (granivory, herbivory, carnivory) and the indirect interactions among the prey species (as in Fig. 3). Figure 3 is derived from the equations I used to calculate *IS* and *DE* which in turn are based on my experimental design. However, it would be interesting to see how applicable this experimental and conceptual framework is to other systems and how much of it actually emerges from theory alone and not just experimental design. Progress could also be made in examining the links between indirect interactions mediated by predators and the abundances, spatial distributions, and coexistence of the prey species (i.e., community structure).

For instance, a logical next step would be to explore whether the indirect interactions documented in this

study have any consequences for the structure of the plant community. One would expect apparent competition among seeds to lead to the spatial disassociation of the species involved in the interaction and perhaps, the local extinction of one or more of the species. Also, given that the seed predators in this system may sometimes disperse seeds to the potential benefit of the plant populations, apparent competition among seeds might actually be beneficial. Rodents might cache the seeds that they harvest from natural patches. If those seeds subsequently germinate then the greater proportion of seeds removed from mixed-species patches than monospecific patches would no longer represent a negative indirect effect; the indirect effect would be positive. This scenario illustrates the potential complexity of indirect interactions in this ecosystem and suggests that the consequences might be difficult to decipher. The community-level consequences of indirect interactions in other ecosystems might be as complex, or the consequences of indirect interactions might pale in comparison to the consequences due to direct interactions. Regardless, future research on the causes and consequences of indirect interactions is very worthwhile.

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#### Appendix 1 The randomization test used to detect indirect interactions

The randomization test was written in TrueBASIC. Copies of the program are available from the author.

The user inputs the following variables (values in parentheses indicate the values for this study): observed mean *IS* value; sample size ( $n=20$ ); number of seeds of each species used in mixed-species tray ( $m=25$ ); number of seeds used in monospecific tray with a low density of seeds ( $s_{low}=25$ ) or a high density ( $s_{high}=125$ ); and number of iterations (1,000). The program then proceeds through the following steps:

1. Selects random number  $A$  from a uniform discrete distribution between 0 and  $f_j$ , where  $f_j$  is the maximum number of seeds surviving in the mixed-species tray and the monospecific tray for a given species at station  $j$ .  $A$  is then divided by  $m$ ; this simulates proportionate seed survival (PSS) in a mixed-species tray.
2. Obtains random number  $B$  by subtracting  $A$  from  $f_j$ .  $B$  is then divided by  $s_{low}$  or  $s_{high}$ ; this simulates PSS in a monospecific tray at either low or high seed density.
3.  $PSS_{single}$  is subtracted from  $PSS_{mix}$  to give a random *IS* value.
4. Steps 1–3 are repeated  $n$  times to get a random dataset of *IS* values.
5. The average *IS* value of that dataset is obtained.
6. Steps 1–5 are repeated for each iteration.
7. The actual *IS* value is compared to the random distribution of average *IS* values. The output of the program is a probability which is the proportion of random *IS* values further from zero than the actual *IS* value.

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