Influence of Heteromyid Rodents on *Oryzopsis hymenoides* Germination

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Abstract

Seeds (caryopses) of *Oryzopsis hymenoides* were a preferred food by species of heteromyid rodents on sandy desert rangelands. The rodents were selective in the type of *Oryzopsis hymenoides* seeds they put in their cheek pouches, rejecting empty seeds and polymorphic forms with reduced germination. The rodents cached some of these highly germinable seeds and emergence of seedlings from these caches was apparently the primary means of stand renewal of *Oryzopsis hymenoides* in these plant communities. Captivity studies with heteromyid rodents showed that germination of roughly 50% of the seeds in the caches was greatly enhanced by the rodent's removal of the indurate lemma, palea, and pericarp that induced dormancy. An estimated 0.02% of the *Oryzopsis hymenoides* seeds produced on a favorable moisture year germinated from rodent caches and emerged as seedlings.

The germination of seeds of *Oryzopsis hymenoides* has been investigated by numerous scientists for at least 50 years (McDonald and Khan 1977). This long-term investment in research underscores both the economic importance of this perennial grass in western North America and the difficulty in enhancing germination of seeds of the species. Robertson (1977) discussed the importance of *Oryzopsis hymenoides* on western rangelands.

Oryzopsis hymenoides seeds will usually germinate if the lemma and palea are removed and the pericarp is broken (Huntamer 1934, Stoddart and Wilkinson 1938, Fendall 1964). Some collections of seeds also have dormant embryos that require cool-moist stratification before they will germinate (Clark and Bass 1970). When *Oryzopsis hymenoides* is seeded on western rangelands the seeds often have been treated with concentrated sulphuric acid to remove the lemma and palea (Plummer and Frischknecht 1952). However, this enhancement technique is difficult because the acid treatment is deleterious, resulting in microbial decomposition of the embryo and endosperm.

Throughout the long history of research on germination of *Oryzopsis hymenoides* no hypothesis has been substantiated on how seeds of this species germinate in nature. The search for a model for natural regeneration has been complicated by the failure until very recently of plant breeders, despite extensive collections and testings, to find accessions of this species that are not inherently dormant (Zemetra 1979). Schemes of microbial decomposition of the lemma and palea, or more realistically, abrasion of the covering structures by saltation of the seeds over sandy-textured soil surfaces, have been proposed. However, *Oryzopsis hymenoides* seeds recovered from desert seedbeds with evidence of sand abrasion have been shown to be less germinable than entire seeds (Young et al. 1983).

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The germination enhancement of various seeds by heteromyid rodents has been reported in the literature (Reynolds 1950, LaTourrette et al. 1971). The seeds of many herbaceous species in western rangelands are collected by those rodents and cached. The caches are in topoedaphic situations that favor germination (Harper et al. 1965). Many of the resulting seedlings are then grazed by the rodents. This scheme of collecting and caching seeds and grazing cotyledons or coleoptiles of the resulting seedlings has been shown to be necessary for adequate carotene, dietary water and vitamin levels in rodent diets for reproduction (Beatley 1969, LaTourrette et al. 1971, Bradley and Mauer 1971).

The purpose of our research was to determine the relationship between the seed collecting and caching activities of heteromyid rodents and *Oryzopsis hymenoides* seed germination.

Methods

The study was located in Desert Queen Valley, in the northern Carson Desert, 80 km northeast of Reno, Nev. The valley was an embayment of pluvial Lake Lahontan, but the lake sediments are buried in sands that eroded from the delta of the Truckee River and are trapped in the valley in the lee of the Hot Springs Mountain Range (Morrison 1964). The sands support excellent stands of *Oryzopsis hymenoides* interspersed among *Sarcobatus baileyi* shrubs growing on small dunes. During certain years the sands are covered with *Oenothera deltoides* in the spring. The valley floor is about 1230 m in elevation and receives about 11 cm of precipitation annually, which occurs primarily as snow during the cold winter months. Within the last decade, the Carson Desert has been invaded by the alien forb *Salsola paulsenii* (Young and Evans 1979). In infrequent years with abundant summer thunderstorms, *Salsola paulsenii* is the dominant herbaceous vegetation. During years with above-average spring precipitation, the alien annual grass, *Bromus tectorum* is relatively abundant around the margins of the valley.

Beginning in January, 1977, rodents were trapped in order to examine cheek pouches for seeds. Snap-traps were baited with a rolled oats-peanut butter mixture and set in lines of 25 stations each, with one rat trap and one mouse trap per station. The stations were spaced 10 m apart. Rodents were trapped for 3 consecutive nights once each month of the year except May, September, and October from 1977 through 1978. The animals were frozen until cheek pouches were examined for seed content, using seeds collected in the area for comparison and identification. Although cheek pouch examinations do not indicate if and where the contents of the pouches were eaten (Reichmond 1975), they do reveal which seeds were taken by the rodents.

The *Oryzopsis hymenoides* seeds that were recovered from rodent pouches from January through May, 1977, were categorized for seed type and incubated at 20°C in dark germinators. Each seed was maintained in an individual petri dish on germination paper and kept moist with tap water. After 2 weeks incubation the number of seeds that germinated was recorded. If the seed had not germinated, the lemma and palea were removed by dissection and the pericarp pricked. After this treatment the seeds were returned to petri dishes and incubated for another week. If at the end of this additional week the seeds had not germinated, an aqueous solution of 50 ppm of gibberellin (GA_3) was added to the germination substrate and the seeds returned for an additional week's incubation.

The type and germination of the seeds recovered from the rodents were compared to type and germination of *Oryzopsis hymenoides* seeds produced at the Desert Queen site in 1976 and with seeds recovered from the soil at this site during the same time period (Young et al. 1983).

In April, 1978, we randomly located 150 plots each 1 m^2 in area in *Oryzopsis hymenoides* communities in Desert Queen Valley. The number of rodent caches with seedlings emerging per cache were recorded. The sand from around and below 14 caches that had *Oryzopsis hymenoides* seedlings emerging was carefully excavated, dried, screened, and the number of seedlings recorded.

To determine if *Oryzopsis hymenoides* clumps were composed of single or multiple plants, we dug up 100 clumps, separated the crowns, and, on the basis of the presence of seminal roots, estimated the number of plants per clump.

A few rodents were live-trapped with Sherman traps and kept in captivity for studies of seed preference, manipulation, and caching. All captivity trials were conducted with *Dipodomys deserti* and *D. merriami.* During captivity studies, rodents were kept individually in rectangular 38-liter glass terrariums with 7 cm of sand on the bottoms and mesh wire tops. We put the rodents on a maintenance diet of rolled oats and sunflower seeds between research trial. For seed preference trials, 4 rodents (1 male and 1 female of each species) were given 10 g rations of seeds of *Oryzopsis hymenoides* and *Salsola paulsenii* in petri dishes nightly for 11 nights. The weight of the seeds utilized during each 24-hour period was determined. This study was repeated twice with different individual rodents using *Oryzopsis hymenoides* only. During these same trials, the number of *Oryzopsis hymenoides* seeds which had been cached and those with their lemma, palea, and pericarp removed were determined. This was done by daily sifting the sands of each terrarium with a series of fine wire screens. Germination tests were conducted on the seeds recovered in comparison to seeds from the same seedlot that were not manipulated by rodents. Tests were conducted at 15, 20, 25 and 30° C for 4 weeks. Seedling emergence tests were conducted in the greenhouse using rodent manipulated and control seeds planted in sand from the Desert Queen site.

Results and Discussion

Rodent Trapping

Of the nearly 1,000 rodents trapped during the year, 850 were heteromyids (seed-eating rodents with external fur-lined cheek pouches). Two species of *Dipodomys,* one of *Microdipodops* and one of *Perognathus* were recorded in the area (Table 1). *Dipodomys merriami* was by far the most abundant species.

Examination of cheek pouches of rodents trapped in this study showed that the seeds used by all species of heteromyids were predominantly those of *Salsola paulsenii,* the alien forb. Other studies have reported that seeds of alien weeds and other annuals constituted the majority of heteromyid cheek pouch contents (Shaw 1934, Reymonds 1958, LaTourrette et al. 1971). However, during July, when *Oryzopsis hymenoides* seeds were mature and

Table 1. Number and monthly average of heteromyid rodents trapped in Desert Queen Valley, Nev. in 1977.

Species	Number caught	Monthly average
Dipodomys merriami	488	54.2
Dipodomys deserti	159	17.6
Microdipodops pallidus	119	13.2
Perognathus longimembris	84	9.3
Total	850	94.3

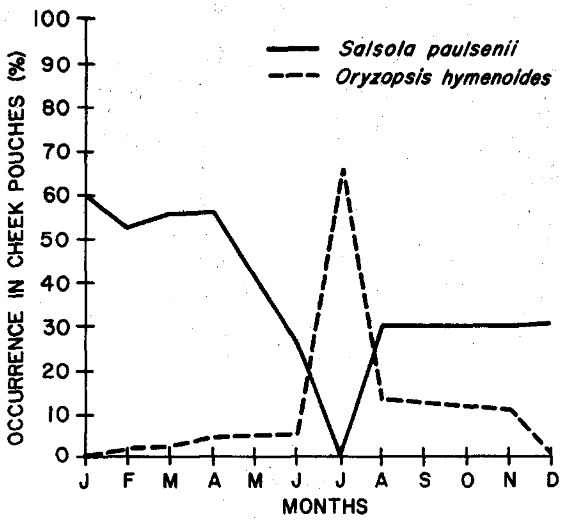

Fig. 1. *Monthly use of seeds of* Salsola paulsenii *and* Oryzopsis hymenoides *by 4 species of heteromyid rodents* (Perognathus longimembris, Microdipodops pallidus, Dipodomys merriami, *and* D. deserti) *in Desert Queen Valley, Nev., during 1977.*

dehisced, no *Salsola paulsenii* seeds were recorded in pouches, and *Oryzopsis hymenoides* seeds dominated (Fig. 1). Use of *Bromus tectorum* and miscellaneous forb seeds was never of major importance. Analyses of food habits for each of the 3 most abundant rodent species (taken individually) showed the same increase in the use of *Oryzopsis hymenoides* seeds in July for each species with a corresponding decrease in *Salsola paulsenii* seed utilization. We concluded that *Oryzopsis hymenoides* seeds were preferred when available. This conclusion is strengthened by the fact that though trapping intensity was the same in June, July, and August, significantly ($P \leq 0.05$) fewer heteromyids were caught in July. According to Fitch (1954), rodents are not as attracted to artificial bait in traps when preferred natural food sources are available.

Seeds Recovered from Rodents

We compared the type and germination characteristics of *Oryzopsis hymenoides* seeds recovered from rodents with a random sample of seeds harvested at the site during the previous season, and with seeds recovered from the surface 15 cm of the soil. This comparison revealed that rodents were selective in the type of *Oryzopsis hymenoides* seeds they carry in their pouches (Table 2). Only 34% of the *Oryzopsis hymenoides* seeds harvested were found to be germinable, compared to 38% of the seeds recovered from the soil and 94% of the seeds recovered from the rodent pouches. We

Table 2. Comparison of seed types and germination parameters of *Oryzopsis hymenoides* seeds collected at maturity, recovered from the surface 15 cm of soil, or removed from pouches of rodents trapped at the Desert Queen location.

	Type of recovery		
Seed types and germination parameters	Random sample of harvested seed	Recovery from surface 15 cm of soil	Recovery from heteromyid rodents
Germination (no enhancement)	4	0	2
Germinable (with enhancement)	34	38	94
Apparently germinable but dormant	34	34	4
Empty	28	28	0
Seed types			
Big black	28	41	90
Small black	37	38	8
Brown	34	21	1
Naked	1	0	1

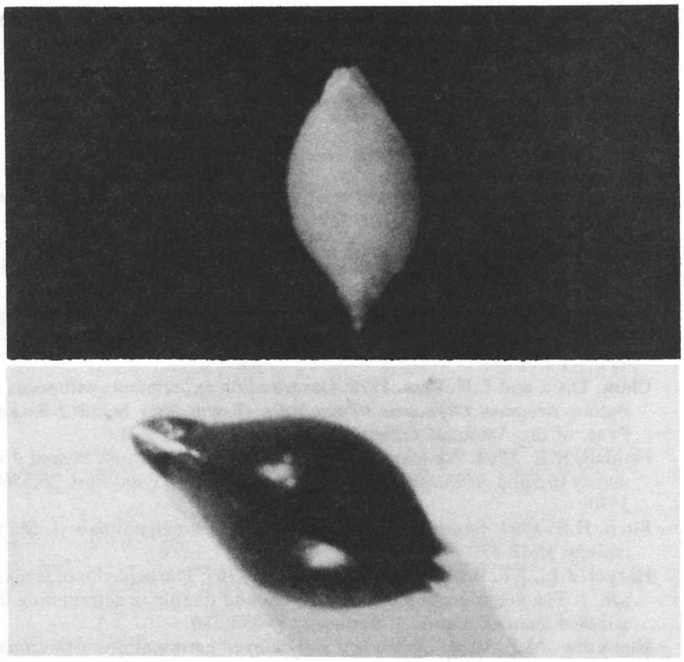

Fig. 2. *(A)* Oryzopsis hymenoides *seeds with lemma and palea removed by rodents and (B) the intact lemma and palea after the seed was removed.*

use germinable to mean the seeds are dormant but will germinate if given enhancement treatments. This in contrast to seeds that germinate without treatment or seeds that fail to germinate after treatment and are classified as dormant. Germinability was determined through the enhancement techniques of removal of the lemma and palea by dissection and addition of 50 ppm of GA_3 to the substrate.

The seeds collected by rodents were only 2% germinable before the enhancement process. Despite the enhancement process, 34% of the harvested seeds and 34% of the seeds recovered from the soil were nongerminable after treatments. In comparison, only 4% of the *Oryzopsis hymenoides* seeds collected by the rodents were nongerminable. Most importantly, 28% of the freshly harvested seeds or those recovered from the soil were empty while none of the seeds picked up by rodents were empty. Reynolds and Glendening (1949) reported that *Dipodomys merriami* in the Southwest apparently test *Prosopsis* seeds for soundness by gnawing.

Orysopzis hymenoides seeds are highly polymorphic and the rodents are selective in the type of seeds they pick up. The seeds recovered from the rodent pouches were 90% big blacks, which constituted only 28% of the current year's production and 41% of the seed reserves in the soil (Table 2). The big black seeds are the largest form of *Oryzopsis hymenoides* seeds. Because they are very plump, these seeds are nearly round in outline. The contrasting form is small black seeds that are longer than wide and much smaller than big blacks. Another major form of these seeds is the brown seeds which include several shapes and shades of color. The rodents picked up very few brown seeds, which constituted 34% of the seeds produced. Rodents are noted for being selective about the types of seeds they pick up, discriminating by size (Brown and Lieberman 1973) or nutritive value (Lockard and Lockard 1971). In our study, the rodents were discriminating between polymorphic forms of the same species.

Seed Caches in the Field

In April, 1978, we found 1.37 rodent caches per m^2 in Desert Queen Valley (Data not shown). About one-third of these caches contained emerging *Oryzopsis hymenoides* seedlings. Most of the caches had been partially excavated by rodents. The mean number of seedlings per cache was 1.4 with a range of 1 to 17 seedlings per cache.

The average cache contained 250 seeds of *Oryzopsis hymenoides* buried at a mean depth of 5.5 cm in the sand. This is near the optimum depth for seedling establishment (Kinsinger 1963, James 1968). Nearly half of these cached seeds were naked, with their lemma, palea and pericarp removed.

We estimated that 3.43×10^6 *Oryzopsis hymenoides* seeds were cached per hectare or about 8% of the seed production of this species at this site in a favorable moisture year (Young et al. 1983).

Oryzopsis hymenoides plants appear to be the typical cespitose perennial grass growing as a solitary bunch. When we dug these bunches at the Desert Queen Valley site, the average number of plants per bunch was 1.2 with a range of 1 to 21 plants per clump. The apparently single plants could be easily separated into components which, based on the occurrence of seminal roots, were often individual plants. There was no clear relation between the size of the bunch and the number of plants. Large bunches often had numerous dead plants mixed with a few living plants.

Captivity Studies

When given free choice between 10 g rations of *Salsola paulensii* and *Oryzopsis hymenoides* seeds, *Dipodomys merriami* and *D. deserti* consumed or cached all of the *Oryzopsis hymenoides* seeds and left about 30% of the *Salsola paulsenii* seeds.

The rodent species consumed an average of 75% and cached 25% of 10 g rations of *Oryzopsis hymenoides* seeds when these seeds were fed alone (Table 3). Of the seeds that were cached, an average of 64% were entire and 36% had their lemma and palea removed. The ratio of naked to entire seeds was in the range recorded for seeds recovered from field caches.

The rodents removed the embryo and endosperm by spreading the lemma and palea without breaking them apart at the calus end of the caryopsis (Fig. 2a and 2b). When the sandy soils at the study site were screened for recovery of seeds 49.4×10^6 per hectare of these separated lemma and paleas were recovered (Young et al. 1983).

Oryzopsis hymenoides seeds that the rodents hulled were markedly more germinable than untreated seeds from the same seedlot—averaging 31% germination. Heteromyid rodents have been known to physically enhance the germination of other rangeland species by breaking seed coats (Reynolds and Glendening 1949). Seeds that were manipulated by rodents, but cached with the lemma and palea entire, did not have enhanced germination. Emergence of seedlings during greenhouse trials in sandy soil also was enhanced by rodents removing the lemma and palea.

Model of Fate of Seeds

From the data available it is possible to illustrate a model of the fate of *Oryzopsis hymenoides* seeds produced at the Desert Queen site (Fig. 3). Note that 28% of the original seed production consisted of empty seeds, and the rodents apparently do not pick up and cache empty seeds. If we subtract the empty seeds then the fate of the 72% of seeds produced is accounted for in our estimates.

The rodents play a selective role at several levels in the scheme. They only pick up filled seeds. The type of seeds recovered from the cheek pouches of the rodents differ in proportion from those noted from seed production. The rodents collected more big blacks which

Table 3. Fate of *Oryzopsis hymenoides* seeds fed to heteromyid rodents in captivity studies. The rodents were fed 10 g of seed (about 5,500 seeds), and after 24 hours the sand in the bottom of their cages was screened and the seeds recovered.

Fate of seeds	Trial #1	Trial #2	Average
	%	%	%
Consumed	74	76	75
Cached	26	24	25
Entire seeds cached	56	73	64
Seeds with lemma and palea removed cached	44	26	36

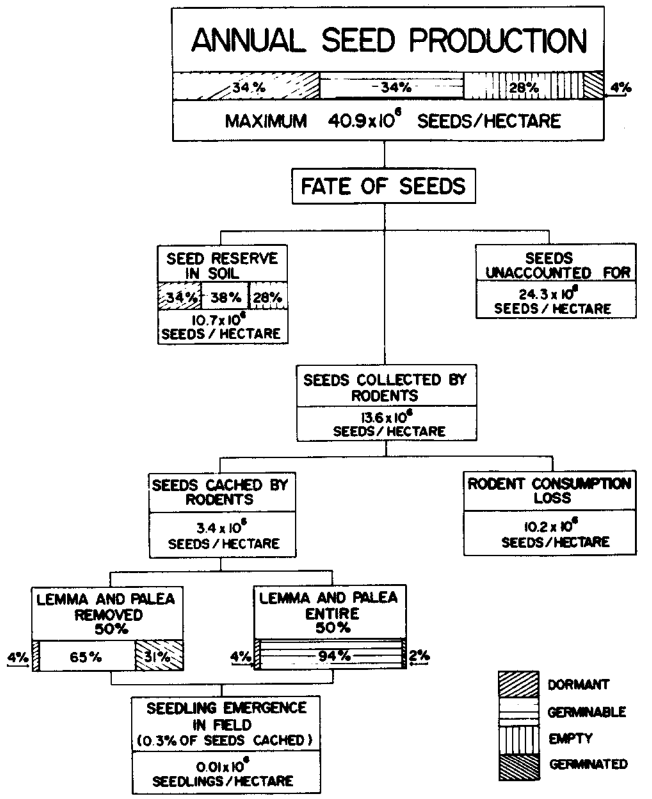

Fig. 3. *Simple model of the fate of* Oryzopsis hymenoides *seeds produced in a desert community and preyed on by heteromyid rodents. Actual germination based on incubation at 20° C. Germinable seeds are those which will germinate after lemma and palea are removed. Seed reserves based on studies by Young et al. (1983), consumptive loss estimate based on captivity studies.*

characteristically have high germinability (will germinate with enhancement) but low initial germination (will germinate without enhancement), but discriminate against small blacks (high germination, low germinability) and especially discriminate against browns (low germination and low germinability).

The activity of the rodent increases the germinability of the seeds that are cached and about one half of the seeds have their lemma and palea removed, insuring roughly 33% actual germination. These seeds are placed in a very favorable microenvironment for germination. One of the largest influences of the rodent populations is that 35% of the filled seed production is consumed.

The rodents also influence the fate of *Oryzopsis hymenoides* when they return to prey on the young plants emerging from the seed caches. The most remarkable feature of this scheme is that 0.02% of the estimated seeds produced in a good year become emerged seedlings. Our observation has shown that the chances of seedlings becoming established plants are extremely small.

We have noted that seedlings emerging in the field from caches often originated from seeds with intact lemmas and paleas. Considering the maximum number of seedlings found per cache was 17 with an average number of seeds per cache at 250, the 7% seedling emergence is within the germination level of untreated seeds. We may find a high percentage of seedlings from seeds with lemmas and paleas entire because the naked seeds in the caches germinate first and these seedlings are readily consumed by the rodents in early spring in an attempt to balance their diets.

Managers of desert *Oryzopsis hymenoides* ranges or individuals interested in rehabilitating disturbed environments with *Oryzopsis hymenoides* should be cognizant of the important interacting role that heteromyid rodents play in the ecology of this species.

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