

Experimental field evidence of interspecific aggression between two species of kangaroo rat (*Dipodomys*)

Robert J. Frye

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

Summary. The competitive coexistence of heteromyid rodents has been primarily ascribed to differential utilization of resources such as microhabitats and seeds. An examination of the use of space by the kangaroo rat *Dipodomys merriami* indicates this species is aggressively subordinate to a larger species, *Dipodomys spectabilis* and is excluded from the larger species home range during the critical fall harvesting season. These experiments suggest that interspecific aggression may be involved in the coexistence of these species. Additional evidence is presented that small scale spatial variations in resource productivity may promote the coexistence of these two species.

Introduction

During the past twelve years ecologists have focused considerable attention on elucidating the structure of Heteromyid rodent communities (see Brown, 1979 and Rosenzweig, 1977 for reviews). Three major hypotheses regarding the mechanisms of competitive coexistence have emerged from these efforts: differential microhabitat selection (Rosenzweig and Winakur 1969; Brown 1973; Brown and Lieberman 1973; Rosenzweig 1973; Brown 1975; Schroder and Rosenzweig 1975; Lemen and Rosenzweig 1974; Whitford 1978), seed size selection (Rosenzweig and Sterner 1970; Brown and Lieberman 1973; Smigel and Rosenzweig 1974; Mares and Williams 1977; Hutto 1978; Lemen 1978), and seed distribution (clump size) selection (Wondolleck 1975; Reichman and Oberstein 1977; Hutto 1978; Price 1978; Frye and Rosenzweig 1980). These hypotheses implicitly assume that the fundamental nature of the competitive process is exploitative. My own initial research (Frye and Rosenzweig 1980) was also based on this assumption. The inadequacy of my research to explain the competitive coexistence of *Dipodomys spectabilis* (120 gm.) and *D. merriami* (40 gm.) led me to reevaluate this assumption and I subsequently hypothesized that direct interference competition may play a role.

The aggressive nature of Heteromyid rodents under laboratory conditions has been documented for the last thirty years (Bartholemew and Caswell 1951; MacMillen 1964; Bateman 1967; Christopher 1973; Congdon 1974; Blaustein and Risser 1976; Ambrose and Meehan 1977) and is well known to all who have kept these species in the laboratory.

Evidence of aggression between Heteromyids under field conditions has also not been lacking, although these data

are of an inferential or anecdotal nature. Grinnell (1932) noted that *Dipodomys ingens*, the largest of the kangaroo rats, was found only in exclusive areas devoid of any other nocturnal granivorous rodent species even though *D. nitratoides* and *D. heermanni* (Tappe 1941; Hawbecker 1944) could be found immediately adjacent to these exclusive areas. Further, Shaw (1934) observed *D. ingens* attack and drive off an individual of the genus *Peromyscus*. Such chases have also been noted between *D. merriami* and *D. microps* (Kenagy 1976) and *D. merriami* and *Perognathus amplus* (Wondolleck 1975). Observing a baited area, Congdon (1974) found that *D. deserti* chased the smaller *D. merriami* and both kangaroo rats would drive off the confamiliar *Perognathus longimembris*.

Stronger evidence of interspecific aggression was gathered by Wondolleck (1978) during a foregoing microhabitat study. He found when he removed *D. merriami*, *Perognathus amplus* – which in the presence of *D. merriami* avoided open habitats – altered its response: it used the open microhabitat to an extent equal to the other microhabitats recognized in his study. Recently, Cliff Lemen and Patricia Freeman (pers. comm.), using removal experiments, have found that when *D. merriami* and *D. ordii* were removed from an area, *Perognathus* species invaded within two weeks.

Strong evidence does exist for the occurrence of intraspecific aggression within populations of *D. spectabilis*. Schroder and Geluso (1973) found that active *D. spectabilis* mounds were uniformly distributed. Using radiotracking techniques, Schroder (1979) then demonstrated that individual *D. spectabilis* occupy intraspecifically exclusive territories.

This evidence led me to conduct preliminary live trapping experiments. The results, though not statistically significant, reinforced my suspicions and I designed the following experiments. Here, will present evidence that the competitive interaction between these two species of *Dipodomys* is primarily by direct interference and is seasonal in occurrence.

Methods

Research site and general field procedures

Experiments were performed in the San Simon Valley, Cochise Co., Arizona; approximately 7 km. ESE of Portal, Arizona. Located at an elevation of 1,350 m, this desert grassland receives an average of 850 mm precipitation an-

nually, 65% of which occurs during May through October (primarily July through September). This pattern of precipitation results in two flowering seasons; the highly predictable late summer season and the less predictable spring flowering.

The experimental procedures were developed during two preliminary exposures during April and June of 1980. Data reported here were acquired during August and October of 1980. The experiments performed during these two months were conducted at two different sites separated by about 4 km. After completion of the experiment in October the experiment was performed at the August site for two nights with results especially identical to the data obtained at the October site.

Experimental procedures

To determine the feeding rates of *D. merriami* in the presence and absence of *D. spectabilis*, I devised and constructed small feeding stations that permitted access of *D. merriami* to seeds but prevented exploitation by the larger *D. spectabilis*. The feeding stations (seed cages) had a 5 cm × 2.5 cm × 20 cm wood base and 6.25 mm mesh hardware cloth as the cage itself projecting about 7.5 cm above the base. At both ends of the cage 2.5 cm × 3 cm holes were cut into the hardware cloth. Laboratory trails affirmed that the holes allowed access by *D. merriami* yet excluded *D. spectabilis*. A 2.5 cm radius × 5 mm depression was drilled into the center of the base to act as a repository for the 1 gram of millet seed placed in each cage. Another hole was cut into the hardware cloth directly above the seed repository to facilitate replacement of exploited seed.

In the general area in which the experiment was to be performed, approximately one hundred apparently active *D. spectabilis* mounds were live-trapped to determine the presence of resident *D. spectabilis*. These mounds were located in two adjacent areas separated by about 100 m. A flip of a coin determined which area was to be used as the removal treatment and which the control. Ten mounds in each area on which *D. spectabilis* were trapped were chosen as replications. The occupied mounds used in these experiments were separated by at least 50 m. On the control plot, captured individuals were released whereas captured individuals on the removal plot were retained until the conclusion of the experiment. Removal mounds were live-trapped every night for the duration of the experiment with two 25 cm × 7.5 cm × 7.5 cm folding Sherman live traps and one 40 cm × 12.5 cm × 12.5 cm wire mesh National trap. Captured *D. merriami* were released at the point of capture on both plots.

Three seed cages were arbitrarily positioned around each of the twenty mounds; one at approximately 4 m from the center of the mound, one at 7 m and a third at 11 m. Seed cages were positioned flush with the ground to prevent rocking and were secured to two large nails driven into the ground to prevent upset of the cage by *D. spectabilis*. Seed cages were supplied with millet seed every afternoon at sundown and were checked at sunrise. Exploited seed was replenished at sundown.

The maximum distance at which the seed cages were positioned was based on two criteria. Schroder (1979) found that the average size of the area in which *D. spectabilis* spent 95% of their activity time was 450 m². This corresponds to a circular area with a radius of about 12 m. The

second criteria was a simple model of the energetic requirements and expenditures of an individual rodent. I calculated that given plant, flower and fruit density of a nearby, generally more depauperate area (R. Inouye, pers. comm.), an individual *D. spectabilis* could persist on a circular territory with a radius of about 10–14 m for one year.

While developing the field procedures in April and June, I noted that the trappability of *D. merriami* seemed to vary with the changes in the density of *D. spectabilis* mounds and with the apparent density of seed resources. In a preliminary attempt to measure these possible relationships, I sampled both plant density and *D. spectabilis* mound density in the four areas on which I had performed removal experiments. Plant density was sampled by censusing and collecting all plant material within 0.25 m² square plots. Five samples were taken at 50 m intervals at each of the four sites. (Three sites were within 1.6 km of each other while the fourth site, the October site, was about 4 km from the other three.) Active *D. spectabilis* mound densities were determined by counting the number of mounds within a 200 m × 200 m plot. In addition, nearest neighbor distances were determined for all active mounds found on these plots.

Results

The data reported here are frequencies of utilization or lack of utilization of the seed cages. I found that fractional utilization of the 1 g of millet seed in each cage was rare and in virtually all cases it appeared to have been caused by wind disturbance of the seeds. Such data are excluded from this analysis.

August

Table 1 presents the results obtained for a two night exposure during August, 1980. A three way chi-square test verified what is clear from inspection of Table 1: the three factors – presence or absence of *D. spectabilis*; distance of seed cages; and exploitation or lack thereof – are independent ($\chi^2 = 12.2$, $P > 0.05$, d.f. = 7). From this result, I have concluded that utilization of seed cages by *D. merriami* was not influenced by the presence of *D. spectabilis*. Apparently, *D. merriami* had free use of the area immediately around *D. spectabilis* mounds.

October

The experiment was repeated October 14–22, 1980. The results of this exposure are reproduced in Table 2. In contrast to the August exposure, the overall three way contingency table test for the October data was significant ($\chi^2 = 25.2$, $P < 0.05$, d.f. = 7) indicating the lack of independence of the three factors. To determine the nature of the

Table 1. Results of territoriality experiment conducted during August, 1980. Plus indicates seed exploited

	Distance (m)						Total	
	4		7		11			
Exploitation	+	0	+	0	+	0	+	0
Treatment								
Removal	7	13	3	17	5	15	15	45
Control	4	16	8	12	12	8	24	36
Total	11	29	11	29	17	23	39	81

Table 2. Results of territoriality experiment conducted during October, 1980. Plus indicates seed exploited

	Distance (m)						Total	
	4		7		11			
Exploitation	+	0	+	0	+	0	+	0
Treatment								
Removal	12	48	8	52	7	53	27	153
Control	0	50	0	50	1	49	1	149
Total	12	98	8	102	8	102	28	302

Table 3. Standardized residuals, d_{ij} , of the test of independence of treatment and exploitation. The terms, d_{ij} , are approximately normally distributed with mean 0 and standard deviation 1

Treatment	Exploitation	
	+	0
Removal	4.6	-4.6
Control	-4.6	4.6

dependence, I performed a test of partial independence between distance and the other two factors. This test of partial independence was not significant ($\chi^2 = 3.8$, $P > 0.05$, d.f. = 6). Given this result and the overall lack of independence I was able to compress the contingency table along the distance factor and examine the independence of treatment (*D. s.* present or absent) and exploitation by the procedures of Everitt (1977). As I expected, this test indicated a lack of independence ($\chi^2 = 21.5$, $P < 0.05$, d.f. = 1). An examination of the standardized residuals (Table 3) reveals that control seed cages were significantly underexploited while removal seed cages were significantly overexploited. From these results I have concluded that during October *D. spectabilis* inhibits foraging by *D. merriami* within its home range.

In addition to these experiments, I also attempted to determine the frequency of utilization of seed cages by *D. merriami* when the seed cages were placed in an area used by *D. merriami* but not *D. spectabilis*. The area used was at least 75 m from the nearest occupied *D. spectabilis* mound. I call this frequency the basal exploitation frequency.

I compared the basal frequency to the utilization frequency of both control and removal seed cages. The overall contingency table comparison was significant ($\chi^2 = 22.2$, $P < 0.05$, d.f. = 2). I then subdivided this table to make two single degree of freedom comparisons between the basal exploitation and the removal and control exploitation frequencies. These tests indicated no difference between the basal and removal frequencies ($\chi^2 = 0.1$, $P > 0.05$) while control and basal frequencies were significantly different ($\chi^2 = 17.7$, $P > 0.05$).

Discussion

Though I maintain that the data are evidence that direct interference plays a role in the competitive coexistence of

these two species, the simple result that *D. merriami* will use an area after *D. spectabilis* is removed is not a unique prediction from an interference hypothesis. If two competing species interact indirectly through exploitation mechanisms removal of one species may result in invasion and utilization of that species former foraging area. How then can I distinguish between the two fundamental assumptions within the context of my experimental design?

Through hypotheses based on the two different assumptions both predict invasion and utilization of formerly apparently exclusive areas, the two assumptions do predict different time scales of response. If the nature of the competitive interaction is exploitation such that one species avoids a second species foraging area due to depression of resources, the invasion rate of the second species must be tied directly to the renewal rate of the resources in question. The slower the renewal rate of resources the slower the response of the second species. In contrast, if the nature of the interaction of the two species is by direct interference, removal of the dominant species should result in an immediate response from the subordinate species. This is the result I obtained for the October experiment. A goodness of fit χ^2 test of the nightly frequency of exploitation on the removal mounds using a null hypothesis that the frequency of use was the same for all nights of the experiment was not significant ($\chi^2 = 2.1$, $P > 0.05$, d.f. = 5). This implies that the response of *D. merriami* was the same the first night as compared to all subsequent nights. Under the assumption of an exploitative interaction this could only occur if seeds were completely renewed within twenty-four hours. Though the renewal rate of seeds under desert conditions is not known, the likelihood that complete renewal occurs within twenty four hours is vanishingly small.

The two basic assumptions of exploitation and interference also lead to quantitatively different predictions regarding the use of seed cages on the control mounds. If direct interference mediates the interaction of the two species the control seed cages should be unexploited since *D. spectabilis*, the dominant species, will prevent incursion of *D. merriami* into its foraging area. The assumption of exploitation however predicts that though *D. merriami* will not forage in the depleted *D. spectabilis* foraging area, they will not be prevented from travelling through these areas thus encountering the control seed cages. The exploitation frequency of the control seed cages should be proportional to the activity of *D. merriami*. The almost total lack of exploitation of the control seed cages is consistent with the assumption of interference.

Given the apparent behavioral dominance of *D. spectabilis* and its ability to exclude *D. merriami* for at least some time of the year, why are both species found in the same area?

A simple possible answer to this question involves the small scale heterogeneity in fall plant density. Assuredly, all *D. spectabilis* individuals will not possess home ranges of equal value. Some areas may simply not be able to support an individual *D. spectabilis*. These areas would then be open for use by *D. merriami*.

My hypothesis leads to a number of predictions. If small scale spatial heterogeneity plays a role in coexistence, I would expect that as the variation in plant density increases, the density of active *D. spectabilis* mounds would decrease as would the mean nearest neighbor distance increase. This variation should also result in higher trappability of *D. mer-*

Table 4. Removal treatment site characterization for four sites used during 1980

Site	Coefficient of variation of plant density	<i>D. spectabilis</i> mounds		<i>D. merriami</i> trap success (captures/100 trap nights)
		density (No./ha.)	\bar{X} nearest neighbor (m.)	
April	128.5	7.0	22.8	16.7
June	56.3	11.9	14.7	2.5
August	61.5	8.6	17.1	12.5
				(10.0) ^a
October	57.8	10.0	15.9	3.3

^a Trap success on site during October

riami. These predictions are verified by the data I have gathered at the four sites on which I set up removal plots (Table 4). Spearman rank correlation of the coefficients of variation of plant density and the density of active *D. spectabilis* mounds was significant ($r_s = -1$, $P = 0.04$, $n = 4$) as was the correlation with mean nearest neighbor distance ($r_s = 1$, $P = 0.04$, $n = 4$). In addition, the correlation of the coefficient of variation of plant density and the number of *D. merriami* captured per one hundred trap nights was significant ($r_s = 1$, $P < 0.05$, $n = 5$).

These experiments, as with any experiment, may include certain possible errors that could have influenced the results obtained. The first possible experimental error does not affect the interpretation of these results. My seed cages allow the entrance of *D. merriami* and any smaller species. Although not critical to the results, I maintain that *D. merriami* was the primary exploiter based upon several observations. In the first place, smaller species were relatively rare; less than 100 individuals of smaller species were trapped in over 5,000 trap nights over 4 years. Secondly, attempts to determine species identities by observing tracks made in smoothed dust around the seed cages resulted in no tracks inconsistent with those made by species of *Dipodomys*.

Another possible source of error involves differences in density of *D. merriami* on the control and removal plots. Arguing against this possibility is the uniformity of the habitat in which both treatments were situated. The preliminary trapping experiment conducted in 1978 was performed on the exact site as the October, 1980 experiment. At that time the density of *D. merriami* was virtually identical between the two treatments. In addition, before the experiment was initiated in October, three hundred twenty trap nights on the two treatments resulted in the capture of five *D. merriami* on the control treatment and no *D. merriami* on the removals. Such low numbers of *D. merriami* are not usual and may be explained by noting that two hundred forty of the trap nights were in the immediate vicinity of *D. spectabilis* burrows. In the future more extensive characterization of *D. merriami* density will be undertaken.

One other possible source of error was the use of bait and traps on the removal treatment while the control treatment was not trapped. Though unlikely, it may be possible that the bait present on the removal mounds drew *D. merriami* into the area round *D. spectabilis* burrows in greater numbers than on the control burrows. Future exposures will include bait and closed traps on the control burrows.

In conclusion, simple field experiments have shown that during at least one time of year *D. spectabilis* excludes

D. merriami from its home range. Hence, interspecific aggression may be involved in the coexistence of these two species. In addition, preliminary characterization of small scale spatial variation in plant density, *D. spectabilis* mound density and the trappability of *D. merriami* suggest that the local coexistence of the two species may be mediated by spatial variation in resource density.

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