Relationships between environmental variation and the reproductive biology of Ord's kangaroo rat *(Dipodomys ordii)*

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Summary. — The 1739 Ord's kangaroo rats (*Dipodomys ordii* Woodhouse) collected during the 25-month study were classified into three age groups using cranial characters. Based upon size of testes, males were reproductively capable throughout the year. Peak breeding periods for females occurred October 1978-March 1979, June 1979, August-October 1979, and January-March 1980. The average number of embryos per pregnant adult female was 2.5 and for nonadults 2.2. There were significant correlations between the reproductive characters and 14 environmental variables. It is postulated that reproductive seasonality may be related to the effects of rainfall upon female kangaroo rats. These findings are in concordance with past studies that established a relationship between the presence of green vegetation and *Dipodomys* reproduction.

Résumé. — Au cours de 25 mois d'étude, 1 739 rats-kangourous (*Dipodomys ordii* Woodhouse) ont été collectés. Ils ont été répartis en 3 classes d'âge d'après les caractères de leurs crânes. D'après les dimensions des testicules, on constate que les mâles ont pu se reproduire pendant toute l'année. Les femelles ont été particulièrement fertiles d'octobre 1978 à mars 1979, en juin 1979, d'août à octobre 1979 et de janvier à mars 1980. Les femelles adultes ont en moyenne 2,5 embryons, tandis que les femelles subadultes en ont 2,2. Il y a des corrélations significatives entre les caractéristiques de la reproduction et 14 variables du milieu. La saison de reproduction des femelles est surtout en rapport avec les effets de la saison des pluies d'automne. Ceci confirme les résultats d'anciennes études qui établissaient une relation entre la reproduction des *Dipodomys* et la présence de végétation verte.

INTRODUCTION

Hoditschek and Best (1983) reviewed the reproductive biology of Ord's kangaroo rat (*Dipodomys ordii* Woodhouse). Though previous studies indicate that season of reproduction varies considerably within the geographic range of this species, the association of environmental variables with reproductive events indicates there is also annual variation in breeding seasonality. Annual variation

in reproductive seasonality for *Dipodomys* may be related to rainfall and its effect upon food production (e.g., McCulloch and Inglis 1961 ; Beatley 1969 ; Bradley and Mauer 1971 ; Kenagy 1973 ; Soholt 1977).

Hoditschek and Best (1983) found the reproductive characters they studied were highly correlated, thus non-histologic examination of tissues would provide accurate reproductive data and simultaneously would reduce the time and financial costs. External measurements of testes appear to give as reliable a measure of reproductive capability as histologic sections (Hoditschek and Best 1983). Embryo counts and size of ovaries are similarly adequate indicators of female reproduction, so it is reasonable to use these to determine reproductive seasonality. Data on numbers of corpora lutea and the potential loss of ova, however, can most accurately be determined histologically.

The reproductive biology of *D. ordii* has been addressed in New Mexico (Bailey 1931 ; Blair 1943 ; Johnston 1956) and west Texas (Garner 1974), but no studies have been conducted in the extensive shinnery oak-mesquite habitat of southeastern New Mexico.

Non-histologic examinations of male and female reproductive tissues were used to investigate : 1) differences in reproductive characters among age groups ; 2) the seasonality of reproduction ; and 3) relationships between changes in reproductive intensity and environmental parameters.

MATERIALS AND METHODS

From March 1978 through March 1980, 1739 *D. ordii* (865 males, 874 females) were kill-trapped approximately 40 km E of Carlsbad, Eddy Co., New Mexico (within a 8 km radius of drill hole ERDA 9, SE corner, Sec. 20, T22S, R31E). Specimens were collected in a shinnery oak-mesquite association *(Quercus havardi-Prosopis glandulosa)*. Although shinnery oak and mesquite did not have the greatest density on our study area, they were among the most obvious plant taxa. Extensive vegetation analyses of this non-cultivated region have been conducted by W.C. Martin of The University of New Mexico (see Best and Jackson 1982).

Museum study skins, skulls, and reproductive organs (preserved in 10 % neutral formalin) were deposited in the Eastern New Mexico University Natural History Museum, Portales. Except for 135 specimens with misplaced skulls, animals were classified as adults, subadults, or juveniles according to the cranial criteria of Best and Schnell (1974). The remaining 135 specimens (7.5 % of the total) were aged using the three male and three female reproductive characters in discriminant analyses (Nie *et al.* 1975). A total of 26 samples was collected during the study. Sample number, collection dates, and month of environmental data used in analyses were :

1) 12-27 March, March 1978 ; 2) 8-16 April, April 1978) ; 3) 5-17 May, May 1978 ; 4) 2-9 June, June 1978 ; 5) 28 June-2 July, July 1978 ; 6) 30 July-12 Aug., Aug. 1978 ; 7) 25 Aug.-10 Sept., Sept. 1978 ; 8) 23 Sept.-8 Oct., Oct. 1978 ; 9) 27 Oct.-5 Nov., Nov. 1978 ; 10) 24 Nov.-3 Dec., Dec. 1978 ; 11) 29-30 Dec., Jan. 1979 ; 12) 15-27 Jan., Jan. 1979 ; 13) 23-24 Feb., Feb. 1979 ; 14) 23-24 March, March 1979 ; 15) 20-22 April, April 1979 ; 16) 24-29 May, May 1979 ; 17) 22-23 June, June 1979 ; 18) 20-29 July, July 1979 ; 19) 15-26 Aug., Aug. 1979 ; 20) 21-23 Sept., Sept. 1979 ; 21) 12-13 Oct., Oct. 1979 ; 22) 12-14 Nov., Nov. 1979 ; 23) 13-15 Dec., Dec. 1979 ; 24) 11-12 Jan., Jan. 1980 ; 25) 15 Feb., Feb. 1980 ; 26) 14-15 March, March 1980.

One preserved testis of each male was trimmed of non-testicular tissue, weighed, and measured (length and width) to the nearest 0.1 mm with dial calipers. For females, embryos were counted and the entire reproductive tract was preserved. The length and width of both preserved ovaries were measured to the nearest 0.1 mm using dial calipers, and these four ovarian measurements were then added together and divided by four, yielding an average ovarian size.

Monthly means, sample sizes, and standard deviations of reproductive characters for each age group of males and females were determined. A single classification analysis of variance was used to compare age groups as well as months within each age group. The sums-of-squares simultaneous test procedure (SS-STP : Gabriel 1964 ; Gabriel and Sokal 1969) was used to determine which months and ages composed statistically nonsignificant subsets for each character.

Pearson product-moment correlation coefficients (Nie *et al.* 1975) were calculated between each of the reproductive characters and each of several environmental variables obtained from the nearest weather stations. Three groups of environmental data were used : 1) 30-year monthly means for temperature, precipitation, heating degree days, and cooling degree days at Carlsbad (NOAA 1973) ; 2) seven monthly temperature characters (average maximum, average minimum, monthly average, highest, lowest, degree days above 32° C, and degree days below 0° C at Duval Potash Mine ; NOAA 1977-1980) ; and 3) five monthly precipitation characters (monthly total, greatest daily, days with 0.3 cm or more, days with 1.3 cm or more, and days with 2.5 cm or more at Duval Potash Mine ; NOAA 1977-1980). Duval Potash Mine is located about 20 km from our study site.

Comparisons were also made between each reproductive character and each of the environmental variables for the previous month (e.g., May 1978 reproductive data were compared to April 1978 environmental data, etc.). The rationale behind these comparisons was that reproductive characters observed during one month might be related to an environmental event of the previous month. Thus, 32 environmental characters were used in the analyses ; 16 from the same month as reproductive characters and 16 from the previous month.

RESULTS AND DISCUSSION

Results of the SS-STP tests between ages showed that adults differed from nonadults in all reproductive characters. Thus, grouping of adult and nonadult data was inappropriate. Data were meager for several monthly samples of subadults and juveniles, as samples were composed primarily of adults throughout the year. Nonadults were found in every sample, but juveniles were absent in Samples 1 and 4 (March and June 1978) and 17 and 18 (June and July 1979). The greatest numbers of nonadults were present in Samples 12-15 (January through April 1979) ; these samples followed the largest peak period of pregnancy (Fig. 1).

INTRASEXUAL VARIATION

Males.

Hoditschek and Best (1983) found that testes 6.8 mm or longer and weighing 0.07 g or more usually contained spermatozoa. We assumed a similar relationship

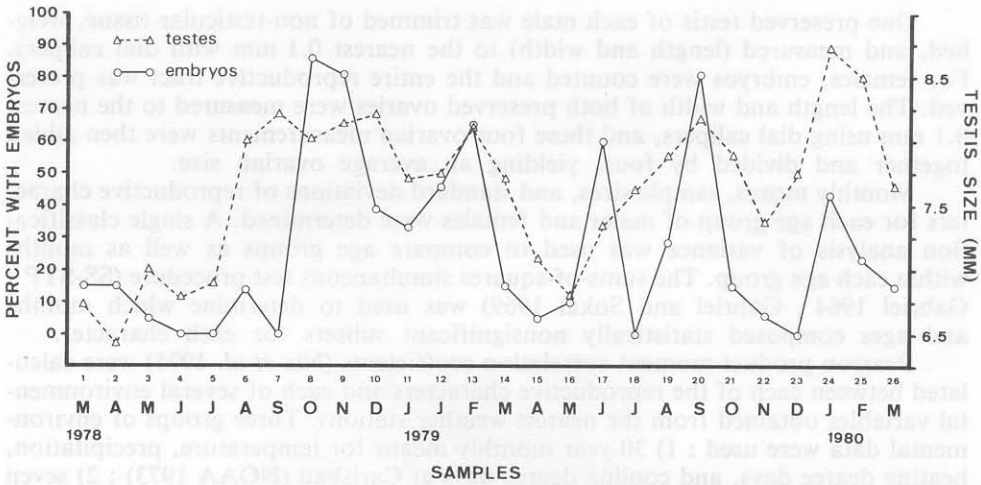


Fig. 1. — The percentage of adult female *Dipodomys ordii* with embryos, and average testis size (testis length + testis width/2) of adult male *D. ordii* from southeastern New Mexico. These two characters were significantly correlated when samples were compared ($r = 0.467$, $P < 0.01$) and when testis size from the previous sample was compared to the percent of pregnant females ($r = 0.469$, $P < 0.01$).

in testis length and weight existed in our samples from southeastern New Mexico. All samples of adults in the present study had means greater than these minima (Table 1).

The results of the analyses of variance indicated highly significant intergroup heterogeneity for both characters (Table 3). SS-STP analyses for the male characters showed that both varied considerably during the study (Table 2). Generally, Samples 1 through 5 and 16 were among the smallest for both characters ; Samples 11, 12, 14, 15, 17, 18, 22, and 23 were somewhat intermediate ; and Samples 7, 9, 10, 13, 20, 24, and 25 were among the largest. This pattern was also shown by the testis size variation depicted in Fig. 1. Testes were larger preceding, or at the same time, peaks in pregnancies occurred for females.

Females.

When the three age groups of females were compared to determine the degree of overlap between reproductive characters, the *F*-ratios were lower than those obtained for males (Table 3), although the two female characters showed significant intergroup variation. The SS-STP analyses showed no overlap between adults and nonadults for number of embryos, but adults and juveniles overlapped subadults in ovarian size.

Females were considered reproductively active if they had embryos. Embryos were present in all but Samples 4, 5, 7, 18, and 23 (Table 1). Since Samples, 5, 7, 18, and 23 preceded samples that had embryos present, females during these months were probably reproductively active or becoming active. Thus, some female reproductive activity was probably present for each sample period. Fig. 1 depicts the percent of pregnant females in each sample. Four peaks of pregnancies occurred during the study, i.e., Samples 8-14 (October 1978-March

TABLE 1. — Reproductive characters for 26 samples of adult male and female *Dipodomys ordii* from southeastern New Mexico. Measurements presented are mean (sample size ; standard deviation). See text for collection dates.

Sample	Testis characters for males		Characters for females	
	Length(mm)	Weight(g)	Embryos	Ovary size (mm)
1	8.6(23;1.31)	0.13(23;0.06)	0.4(11;0.81)	1.8(11;0.50)
2	8.4(27;1.14)	0.11(26;0.05)	0.5(18;1.30)	1.4(15;0.22)
3	8.8(29;1.04)	0.14(27;0.04)	0.2(20;0.67)	1.7(15;0.56)
4	9.0(15;0.98)	0.13(14;0.06)	0.0(13;0.00)	1.6(11;0.20)
5	9.2(11;1.00)	0.15(11;0.03)	0.0(28;0.00)	1.6(28;0.19)
6	10.0(13;1.00)	0.21(12;0.06)	0.4(7;1.13)	1.5(7;0.56)
7	10.2(30;1.17)	0.21(27;0.04)	0.0(16;0.00)	1.7(16;0.22)
8	10.2(25;0.84)	0.22(25;0.04)	2.6(22;1.30)	2.0(20;0.24)
9	10.4(12;1.00)	0.24(12;0.04)	2.7(16;1.62)	2.4(15;0.39)
10	10.3(13;1.12)	0.23(13;0.05)	1.7(16;1.58)	2.3(14;0.36)
11	9.9(10;1.31)	0.19(10;0.04)	1.0(12;1.48)	2.1(9;0.44)
12	9.7(15;0.68)	0.20(15;0.04)	1.0(32;1.28)	1.9(30;0.27)
13	10.4(34;1.02)	0.23(34;0.06)	1.6(28;1.28)	2.0(28;0.24)
14	9.9(21;0.88)	0.19(21;0.04)	0.3(33;0.67)	1.6(30;0.27)
15	9.3(11;0.73)	0.15(10;0.05)	0.1(19;0.46)	1.7(18;0.25)
16	9.2(9;0.70)	0.16(9;0.06)	0.3(20;0.64)	1.9(19;0.21)
17	9.6(25;0.95)	0.18(15;0.05)	1.0(5;1.00)	1.8(4;0.15)
18	9.6(25;0.97)	0.19(25;0.04)	0.0(10;0.00)	1.8(9;0.23)
19	10.1(29;0.89)	0.21(22;0.05)	0.6(7;1.13)	1.9(8;0.35)
20	10.5(27;0.86)	0.25(26;0.06)	2.3(27;1.41)	2.3(24;0.24)
21	10.2(24;0.78)	0.21(24;0.05)	0.4(27;1.05)	1.7(26;0.24)
22	9.6(26;1.42)	0.17(26;0.07)	0.1(17;0.24)	1.9(16;0.24)
23	9.9(14;0.91)	0.19(14;0.05)	0.0(20;0.00)	1.7(17;0.18)
24	11.3(37;1.00)	0.24(37;0.05)	0.8(44;0.94)	2.0(43;0.25)
25	11.1(38;1.11)	0.23(38;0.05)	0.5(40;0.85)	2.0(38;0.25)
26	10.2(25;1.22)	0.19(25;0.07)	0.2(27;0.58)	1.8(27;0.27)

1979), Sample 17 (June 1979), Samples 19-21 (August-October 1979), and Samples 24-26 (January-March 1980).

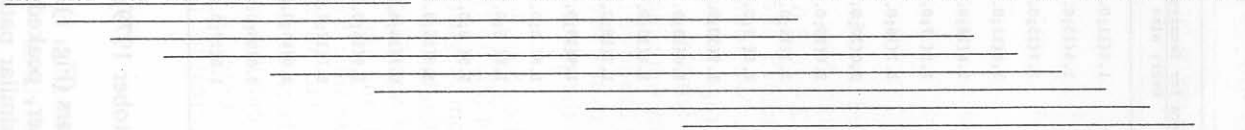
There were some similarities in seasonality between years (Fig. 1). In 1978-1979, breeding peaked in early autumn, dipped in early winter, peaked again in late winter, and decreased in early spring. For 1979-1980, a similar pattern appeared, but the early autumn peak was primarily represented by the Sample 20 pregnancies (September 1979) ; the late autumn-early winter dip was more pronounced, and the late winter increase was not as great as for 1978-1979. Our findings closely agree with those of McCulloch and Inglis (1961), who determined that *D. ordii*

TABLE 2

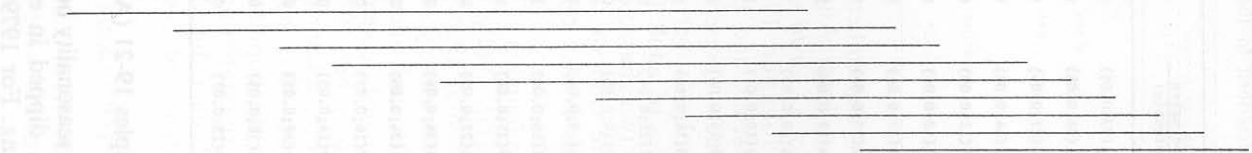
Character — Results of SS-STP analyses

Males

Testis length	24	25	20	9	13	10	7	26	8	21	19	6	14	23	11	12	17	22	18	15	16	5	4	3	1	2
	11.3	11.1	10.5	10.4	10.4	10.3	10.2	10.2	10.2	10.2	10.1	10.0	9.9	9.9	9.9	9.7	9.6	9.6	9.6	9.3	9.2	9.2	9.0	8.8	8.6	8.4

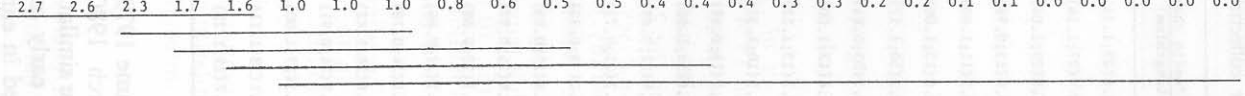


Testis weight	20	9	24	13	10	25	8	19	7	6	21	12	26	11	23	14	18	17	22	16	15	5	3	1	4	2
	0.25	0.24	0.24	0.23	0.23	0.23	0.22	0.22	0.21	0.21	0.21	0.20	0.19	0.19	0.19	0.19	0.19	0.17	0.17	0.16	0.15	0.14	0.14	0.13	0.13	0.11



Females

Embryos	9	8	20	10	13	12	17	11	24	19	2	25	6	21	1	14	16	26	3	15	22	18	7	23	4	5
	2.7	2.6	2.3	1.7	1.6	1.0	1.0	1.0	0.8	0.6	0.5	0.5	0.4	0.4	0.4	0.3	0.3	0.2	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0



Ovary size	9	10	20	11	8	24	13	25	16	22	19	12	18	1	26	17	21	3	7	23	15	14	4	5	6	2
	2.4	2.3	2.3	2.1	2.0	2.0	2.0	2.0	1.9	1.9	1.9	1.9	1.8	1.8	1.8	1.8	1.7	1.7	1.7	1.7	1.7	1.6	1.6	1.6	1.5	1.4

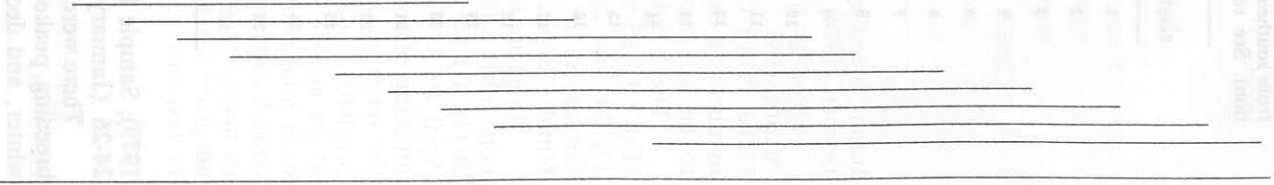


TABLE 3. — Results of single classification analyses of variance for male and female reproductive characters in *Dipodomys ordii*. Comparisons are between three age groups and between 26 samples of adults. Characters are described in the text, * $P < 0.05$; ** $P < 0.001$.

Character	Between age groups d.f.	Between age groups F-ratio	Between samples for adults d.f.	Between samples for adults F-ratio
Males				
Testis length	2,834	663.208**	25,542	12.156**
Testis weight	2,804	369.376**	25,515	12.338**
Females				
Embryos	2,792	15.650**	25,509	14.739**
Ovary size	2,713	5.102*	25,472	12.513**

began breeding during August or September and ended in March. Similarly, Garner (1974) reported parturition from August through May.

Average litter sizes reported for *D. ordii* vary from 2.4 to 3.6 (Bailey 1931 ; Alcorn 1941 ; Day *et al.* 1956 ; Johnston 1956 ; McCulloch and Inglis 1961 ; Flake 1974 ; Garner 1974 ; Hoditschek and Best 1983). We found the average numbers of embryos in adults, which represents the average potential litter size, to be 2.5. Nonadults had 2.2 embryos per pregnant female.

The *F*-ratios for the 26 samples of adult female data were highly significant (Table 3). SS-STP analyses for the two characters (Table 2) showed Samples 8-13, 17, 20, and 24 generally had more embryos and their ovary sizes were among the largest of all the samples. This is also reflected in the percent of pregnant females depicted in Fig. 1.

Pregnant nonadult females were found in 11 samples, i.e., Samples 6 (1 pregnant nonadult), 8 (1), 9 (6), 10 (2), 11 (1), 12 (2), 13 (14), 14 (2), 15 (1), 20 (2), and 26 (1). Of the 33 nonadult pregnancies, 29 occurred from August 1978 through April 1979. This period corresponds closely with the October 1978-March 1979 breeding season observed for adults, and since there was some lag time between the onset of adult breeding in August-September 1978 and the appearance of pregnant nonadults in October-November 1978, it is possible that young bred at an age of 2-3 months. Therefore, adults may have had an early litter and both adults and their offspring may have had litters later in the season. The contribution of new individuals to the populations by nonadults may contribute to maintaining the population, in re-establishing it after times of environmental adversity when populations have been reduced, or in increasing population size in response to an unusual abundance of resources.

CHARACTER CORRELATIONS

Correlation coefficients resulting from comparisons of adult male and female characters showed that male characters were highly correlated with each other

TABLE 2. — Variation in two adult male and two adult female reproductive characters in *Dipodomys ordii* from southeastern New Mexico. Statistically homogeneous subsets derived from SS-STP analyses are shown by lines below the sample numbers and ranked means. Collection dates for each sample are given in the text.

($r = 0.934$; $P < 0.001$). The female characters were also significantly correlated with each other ($r = 0.762$; $P < 0.001$).

Comparisons of male characters with female characters yielded significant correlations between all characters. The highest correlation coefficient was between testis weight and ovarian size ($r = 0.686$, $P < 0.001$) and the lowest was between testis length and number of embryos ($r = 0.427$, $P < 0.05$). Comparisons were also made between female characters and male characters for the previous month. Except for the comparison of testis length to number of embryos, all characters were significantly correlated. The highest correlation coefficient was between testis weight for the previous month and ovarian size ($r = 0.575$, $P < 0.001$), and the lowest was between testis length for the previous month and number of embryos ($r = 0.261$, $P < 0.05$). These findings may indicate that both sexes are affected by the same stimuli, whether environmental, behavioral, or physiological.

Environmental relationships

The importance of environmental factors, especially rainfall, in affecting reproduction in *Dipodomys* has been indicated in several studies (Reynolds 1958, 1960 ; McCulloch and Inglis 1961 ; Chew and Butterworth 1964 ; Beatley 1969, 1976*a*, 1976*b* ; Bradley and Mauer 1971 ; Kenagy 1973, 1976 ; Van De Graaff and Balda 1973 ; Reichman and Van De Graaff 1975 ; Soholt 1977 ; Hoditschek and Best 1983). Some have shown that the consumption of green vegetation made available by seasonal rainfall initiates or maintains reproduction. Perhaps the plant-derived cyclic carbamate, 6-methoxybenzoxalinone, or a similar compound stimulates reproductive activity in *Dipodomys,* as has been shown for *Microtus* (see Sanders *et al.* 1981 ; Berger *et al.* 1981).

Our 1978-1980 sampling period appeared to be "typical" for precipitation and temperature in southeastern New Mexico. Data for Duval Potash Mine, though collected for only 13 years, showed no departures from the mean in temperature or precipitation from 1977 through 1980. For Carlsbad, where weather data have been recorded in excess of 70 years, there were some deviations from the climatologic standard normals for precipitation based upon the period 1941-1970, i.e., there were slight increases in 1977 and 1979, and a considerable increase in 1978 that was mostly attributable to heavy rains in September and November (NOAA 1977-1980).

Hoditschek and Best (1983) indicated that the differences in the percentage of pregnant kangaroo rats in their July 1970 sample compared to that for July 1971, supported their supposition that environmental conditions may affect reproduction in *D. ordii.* They found a statistically significant relationship between the greatest amount of rainfall for a single day during the month and the number of corpora lutea. They concluded that rainfall may be important in generating conditions suitable for maintaining the reproductive condition as well as initiating reproduction. In the present study, we also made statistical comparisons between the same suite of environmental variables as Hoditschek and Best (1983) and our six kangaroo rat reproductive characters.

Table 4 presents the 14 environmental variables that were significantly correlated with one or more of the reproductive characters. The highest correlations were between female characters, particularly ovarian size, and the environmental

variables. Number of embryos were correlated only with monthly precipitation characters for the previous month, whereas, ovary size was correlated only with temperature characters. Significant male character correlations were scattered among

TABLE 4. — Product-moment correlation coefficients between adult male and adult female kangaroo rat *(Dipodomys ordii)* reproductive characters and environmental variables for southeastern New Mexico. Only environmental variables having significant correlations with one or more reproductive characters are presented, * $P < 0.05$; ** $P < 0.01$.

	Males		Females	
Environmental variables	Testis length	Testis weight	Embryos	Ovary size
30-year monthly means				
Temperature	-0.376*	-0.321	-0.251	-0.419*
Heating degree days	0.419*	0.367*	0.216	0.427*
Cooling degree days	-0.248	-0.199	0.261	-0.342*
Monthly temperature				
Average maximum	-0.428*	-0.403*	-0.299	-0.499**
Average minimum	-0.359*	-0.303	-0.215	-0.408*
Monthly average	-0.397*	-0.358*	-0.260	-0.458**
Highest	-0.403*	-0.386*	-0.302	-0.479**
Lowest	-0.248	-0.198	-0.156	-0.374*
°Days above 32°C	-0.295	-0.239	-0.267	-0.369*
°Days below 0°C	0.085	0.194	-0.259	0.344*
Monthly precipitation for previous month				
Total	0.177	0.282	0.394*	0.235
Greatest daily	0.234	0.322*	0.400*	0.291
Days 1.3+ cm	0.206	0.288	0.347*	0.210
Days 2.5+ cm	0.142	0.233	0.445**	0.221

the environmental variables, with most being with monthly temperature characters ; the least were with precipitation data for the previous month. Except for 30-year mean cooling degree days and monthly temperature degree days below 0° C, at least one male and one female character were correlated with each of these 14 environmental variables.

Testis length was correlated with six temperature variables and no precipitation variables. Testis length increased as temperatures decreased. We believe that testis weight changes were a simple reflection of the changes in length of testes and thus represented secondary relationships with environmental variables.

The number of embryos were correlated with precipitation during the previous month (Table 4). As rainfall increased during the previous month, the number of embryos increased. Perhaps rainfall "turns on" the reproductive process for females, copulation takes place, and pregnancy occurs. Conversely, ovarian size was correlated with monthly temperature variation and tended to increase

as temperature decreased. Because the majority of pregnancies occurred during cooler months of the year (Fig. 1), the increase in ovarian size was probably caused by the large corpora lutea left by recently released ova during these months.

Even though testis characteristics varied between months, males were reproductively capable throughout the year. Females appeared to have regulated reproductive seasonality ; when rainfall was not adequate, reproductive activities may have been reduced or ceased. As precipitation increased during the onset of cooler weather, ovulation, copulation, and pregnancy may have been initiated by females. The selective advantage of seasonality regulation by females may be related to the energy expenditure required for gestation and care of offspring. In times of environmental adversity, resources may not be sufficient to sustain the energy requirements of pregnant and lactating females. Thus, there may be a selective advantage in becoming pregnant and caring for offspring in the cool-moist months when green vegetation, seeds, and other resources are most plentiful.

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