



## Isotopic composition of carbon and oxygen in desert fauna: investigations into the effects of diet, physiology, and seasonality

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Carbon and oxygen isotope ratios of bone apatite were measured in 14 endothermic and ectothermic vertebrates native to the Chihuahuan Desert and collected in June and July of 1999 and 2000. The  $\delta^{18}\text{O}$  values of most reptiles were very high, up to 44‰ (standard mean ocean water (SMOW)), some of the highest  $\delta^{18}\text{O}$  values ever measured for an animal. The  $\delta^{18}\text{O}$  values of rodents and birds were lower ( $\sim 32 \pm 5\%$  vSMOW), and the earless lizard *Holbrookia maculata* were the lowest of all species analysed ( $\sim 25\%$ ). Omnivorous grasshopper mice (*Onychomys torridus*) had lower  $\delta^{18}\text{O}$  values than granivorous rodents. Results from oxygen analysis likely reflect variation in diet and body water flux differences between endotherms and ectotherms. Carbon isotope analysis revealed a dramatic shift in diet from  $\text{C}_3$  plants in 1999 to  $\text{C}_4$  plants in 2000 in most rodents and birds. Kangaroo rats and reptiles did not change, having a constant  $\delta^{13}\text{C}$  value indicative of a  $\text{C}_3$ -based diet in both years. This suggests reliance on winter annual plant seed caches for kangaroo rats, but not other rodents. The carbon isotope data can be explained in terms of seasonal differences within and between years in the timing and intensity of the seasonal rainfall events, and the productivity of summer and winter annual plants. This study illustrates that stable isotope analysis is a powerful method for tracking dietary change and feeding behavior in desert vertebrates.

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**Keywords:** stable isotopes;  $\text{C}_3/\text{C}_4$  plants; lizards; rodents; seasonality

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## Introduction

The last two decades have seen an ever-growing number of research problems in ecology and physiology addressed using stable isotope biochemistry (Ehleringer *et al.*, 1992; Hobson & Clark, 1993; Magnusson *et al.*, 1999; Vander Zanden *et al.*, 1999; Wolf & Martinez del Rio, 2000). While the majority of this work has focused on studies of plants, animal physiologists and ecologists have also begun to explore opportunities in stable isotope application (DeNiro & Epstein, 1980; Hobson & Clark, 1993; Kohn *et al.*, 1996; Kelly & Finch, 1998; Cerling & Harris, 1999; Magnusson *et al.*, 1999; Vander Zanden *et al.*, 1999; Wolf & Martinez del Rio, 2000). In this study, stable isotope analyses were made on a Chihuahuan Desert vertebrate community in order to better understand the roles of these animals in the ecology of the region. In the summers of 1999 and 2000,  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of bone apatite were measured for 14 species of rodents, birds, and reptiles native to south-eastern Arizona. Oxygen isotope analysis lends insight into water economy and diet of the species examined, while carbon isotope analysis reflects differences in resource use among and between species.

Daily water turnover, water conservation, water loss, thermoregulatory mechanisms, resource selection, and drinking behavior differ within and between major taxonomic and functional animal groups (Randall *et al.*, 1997). As a result, variation in the  $\delta^{18}\text{O}$  values of endothermic and ectothermic vertebrates native to the same community can be expected. Due to their low metabolic rate, ectotherms require less food and water, and lose less water than endotherms (Randall *et al.*, 1997). Given the low body water turnover of ectotherms, high rates of evaporation result in a higher  $\delta^{18}\text{O}$  value. Given these physiological characteristics, we expect the ectotherms examined to be more enriched in  $\delta^{18}\text{O}$  than endotherms (Kohn *et al.*, 1996).

Carbon isotope analysis is regularly used to quantify contributions of different food sources to animal diets (Cerling & Harris, 1999; Magnusson *et al.*, 1999; Vander Zanden *et al.*, 1999; Wolf & Martinez del Rio, 2000). The  $\delta^{13}\text{C}$  value of an animal is strongly dependent on its diet, ultimately upon the plant source at the lower trophic level. Plant carbon isotope ratios depend most strongly on the photosynthetic pathway employed (Fry *et al.*, 1978). Biochemical differences in the photosynthetic pathways of  $\text{C}_3$  and  $\text{C}_4$  plants result in distinct non-overlapping  $\delta^{13}\text{C}$  values for the two groups (Fry *et al.*, 1978; Ehleringer & Cooper, 1988; Ehleringer *et al.*, 1992; Cerling *et al.*, 1999); plants that use the  $\text{C}_4$  photosynthetic pathway have  $\delta^{13}\text{C}$  values between  $-20.0\text{‰}$  and  $-10.0\text{‰}$ , while those using the  $\text{C}_3$  photosynthetic pathway have  $\delta^{13}\text{C}$  values of  $-34\text{‰}$  to  $-22\text{‰}$  (Ehleringer, 1991). Animals should exhibit carbon isotope values that reflect the proportions of  $\text{C}_3$  and  $\text{C}_4$  plants in their diets. At the field site, summer annual plants are a mixture of  $\text{C}_3$  and  $\text{C}_4$  plants, with  $\text{C}_4$  being dominant, while winter annuals are entirely  $\text{C}_3$  plant type (Qinfeng Guo, pers. comm.). Differences in seasonal rainfall events and resulting ephemeral plant abundance were apparent between 1997 and 2000. We predict that differences in  $\delta^{13}\text{C}$  values of the animals reflect variation in the timing and intensity of these seasonal events, and the differential contributions of  $\text{C}_3$  vs.  $\text{C}_4$  plants to the food chain.

## Methods

### *Sample collection*

Samples were collected in 1999 and 2000 during the last week of June and first week of July at the Brown LTREB site in Cochise County, approximately 7 km north-east of Portal, AZ. The site is situated on a sandy bajada of the Chiricahua mountains and the

vegetation is relatively consistent Chihuahuan desert scrub (for a more thorough description of the site, its biota, and ecology see Brown, 1998). Six species of rodent (*Dipodomys ordii*, *Dipodomys merriami*, *Chaetodipus baileyi*, *Chaetodipus pencillatus*, *Reithrodontomys megalotis* and *Onychomys torridus*), six species of reptile (*Holbrookia maculata*, *Urosaurus ornatus*, *Cnemidophorus uniparens*, *Sceloporus virgatus* and *Sceloporus undulatus*) and two species of bird (*Amphispiza bilineata* and *Spizella breweri*) were collected under UNM-Animal Care and Use permits (between one and 14 individuals of each species, see Appendix 1 for common names). Upon collection, specimens were euthanized with Metafane. Specimens were then sealed in plastic bags, stored on ice, and transferred within 2 days to a freezer held at  $-40^{\circ}\text{C}$ . Within 5 days, samples were thawed and flesh was removed. Skeletons were cleaned using a colony of dermestid beetles.

#### *Carbonate apatite preparation and stable isotope analysis*

Cranial bone samples were individually ground to a fine powder using a shatter box, and soaked in hydrogen peroxide for 24 h to remove reactive organic matter. Samples were separated from excess hydrogen peroxide using vacuum filtration, then rinsed with distilled water and oven-dried at  $100^{\circ}\text{C}$ . Conventional phosphoric acid digestion was used to extract  $\text{CO}_2$  (McCrea, 1950). Approximately 40 mg of sample were reacted with phosphoric acid at  $50^{\circ}\text{C}$  for 12 h. To correct for acid fractionation, an  $\alpha$  value of  $1.009311_{(\text{CO}_2-\text{calcite})}$  was used for determining the  $\delta^{18}\text{O}$  value of the carbonate apatite (Swart *et al.*, 1991).  $\text{CO}_2$  gas was purified cryogenically and measured on a Delta E mass spectrometer. Carbon and oxygen isotope ratios were expressed in conventional delta notation ( $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ ) in per mil (parts per thousand, ‰):

$$\delta_{\text{sample}} = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000$$

where  $R$  is the measured  $^{18}\text{O}/^{16}\text{O}$  or  $^{13}\text{C}/^{12}\text{C}$  molar ratio of the sample or standard (McKinney *et al.*, 1950).

All data are reported relative to Pee Dee Belemnite standard (PDB), defined so that the  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values of (National Bureau of Standards (NBS)-19 are  $-2.2\text{‰}$  and  $1.96\text{‰}$ , respectively (Hut, 1987).  $\delta^{18}\text{O}$  values were converted to standard mean ocean water (SMOW) using the following (Coplen *et al.*, 1983):

$$\delta^{18}\text{O}_{\text{vSMOW}} = \delta^{18}\text{O}_{\text{vPDB}} \times 1.03091 + 30.91$$

Samples were analysed in duplicate, and were generally within  $1.0\text{‰}$  of each other (see Appendix 1). To estimate  $\delta^{13}\text{C}$  values of diet for rodents, the  $\delta^{13}\text{C}$  values of bioapatite was related to the bulk diet using values reported by Tieszen & Fagre (1993), for *Mus musculus*, where bioapatite was  $9\text{‰}$  more enriched than bulk diet:

$$\delta^{13}\text{C}_{\text{diet}} = \delta^{13}\text{C}_{\text{bioapatite}} - 9.0$$

#### *Site precipitation and vegetation analysis*

Precipitation data were collected on site by an automated weather station, and annual plant abundance was censused for the summer and winter seasons from 1997 to 2000. Plant abundance was measured as stem counts on permanent quadrants. Total annual abundance on control plots was calculated for the winter and summer seasons between October 1997 and July 2000. Control plots were selected for analysis, as they are representative of the habitat of the site.

## Results

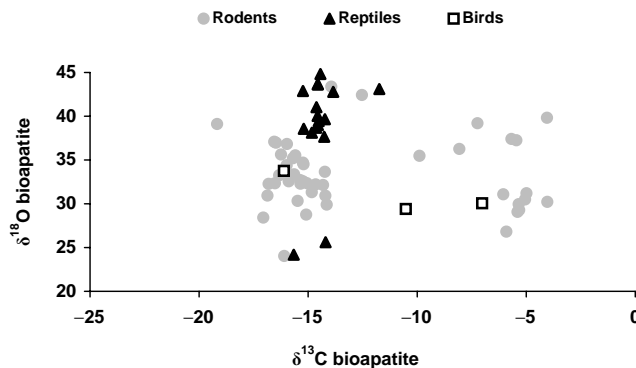
### Oxygen

The  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values of carbonate apatite for animals collected in 1999 and 2000 are shown in Fig. 1.  $\delta^{18}\text{O}$  values of carbonate apatite did not vary between the 2 years. The range of  $\delta^{18}\text{O}$  values for the endotherms, rodents (mean = 33.4‰, S.D. = 3.8‰,  $n = 47$ ) and birds (mean = 31.1‰, S.D. = 2.3,  $n = 3$ ), overlapped (Fig. 1, see Appendix 1). The  $\delta^{18}\text{O}$  values for the two bird species (*A. bilineata* and *S. breweri*) fell just below the mean for rodents (Fig. 1). Among rodents, kangaroo rats (*D. ordii* and *D. merriami*) had the highest  $\delta^{18}\text{O}$  values (mean = 34.5‰), a significant difference from grasshopper mice (*O. torridus*) that had the lowest  $\delta^{18}\text{O}$  values (mean = 29.9‰) ( $t$ -test;  $p = 0.010$ ).

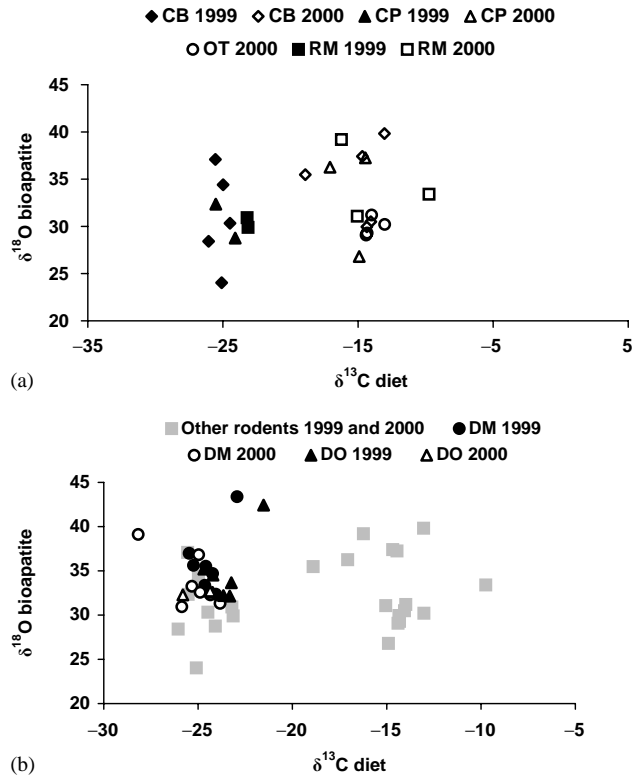
On the basis of the different water-conservation mechanisms, ectotherms should have higher  $\delta^{18}\text{O}$  values than endotherms (Kohn *et al.*, 1996). Our data support this prediction ( $t$ -test;  $p < 0.001$ ), in light of the superb water conservation of lizards. An exceptional outlier was the earless lizard (*H. maculata*). The mean  $\delta^{18}\text{O}$  value of *H. maculata* was 24.9‰, a value 16‰ lower than the mean of other lizards, and the lowest of all species. When *H. maculata* was removed, the difference in  $\delta^{18}\text{O}$  between ectotherms and endotherms increased in significance ( $t$ -test;  $p < 0.0001$ ).

### Carbon

Carbon analyses revealed resource selection within and among species between the two sample periods. A substantial increase in the  $\delta^{13}\text{C}$  values of pocket mice (*C. baileyi* and *C. pencillatus*) and harvest mice (*R. megalotis*) between 1999 and 2000 indicates a shift in diet from  $\text{C}_3$  (−34.0‰ to −22‰) to  $\text{C}_4$  (−20.0‰ to −10.0‰) plant resources (Fig. 2a). These shifts in  $\delta^{13}\text{C}$  values between sample periods were significant: *C. baileyi* ( $t$ -test;  $p < 0.001$ ), *C. pencillatus* ( $t$ -test;  $p = 0.003$ ), and *R. megalotis* ( $t$ -test;  $p = 0.04$ ). Grasshopper mice (*O. torridus*) were collected only in 2000, and also had a  $\delta^{13}\text{C}$  value indicating a  $\text{C}_4$  diet (mean = −13.9‰) (Fig. 2a). In striking contrast, kangaroo rats (*D. ordii* and *D. merriami*) maintained nearly constant  $\delta^{13}\text{C}$  values, indicating a  $\text{C}_3$  diet in both 1999 and 2000 (mean = 24.5‰, S.D. = 1.3,  $n = 23$ ) (Fig. 2b).



**Figure 1.** Values of  $\delta^{18}\text{O}$  vs.  $\delta^{13}\text{C}$  of the carbonate component of bioapatite for all rodents, reptiles, and birds collected in June–July of 1999 and 2000 at the Brown field site, Cochise Co. south-east Arizona. Rodents include: *C. baileyi*, *C. pencillatus*, *O. torridus*, *R. megalotis*, *D. ordii*, and *D. merriami*. Reptiles include: lizards: *H. maculata* (two lowest triangles), *U. ornatus*, *S. virgatus*, *S. undulatus*, *C. uniparens*, snake: *P. melanoleucus*. Birds include: *A. bilineata* and *S. breweri*.



**Figure 2.** (a)  $\delta^{18}\text{O}$  values of carbonate component of apatite *vs.*  $\delta^{13}\text{C}$  values of diet (converted from bioapatite by subtracting 9‰) for rodents collected in June–July of 1999 and 2000, exclusive of kangaroo rats. Individuals collected in 1999 are depicted in black; those collected in 2000 are depicted in white. (CB = *C. baileyi*, CP = *C. pencillatus*, OT = *O. torridus* and RM = *R. megalotis*). (b)  $\delta^{18}\text{O}$  values of carbonate component of apatite *vs.*  $\delta^{13}\text{C}$  values of diet (converted from bioapatite by subtracting 9‰) for all rodents collected in June–July of 1999 and 2000. Triangles and circles depict the two species of kangaroo rat. Black represents individuals collected in 1999, white represents individuals collected in 2000. All other rodent species are depicted by gray squares. (Kangaroo rats: DM = *D. merriami*, DO = *D. ordii*; other rodents: *C. baileyi*, *C. pencillatus*, *O. torridus* and *R. megalotis*).

In addition to kangaroo rats, all ectotherms maintained  $\delta^{13}\text{C}$  values characteristic of a  $\text{C}_3$ -based diet in both 1999 and 2000 (mean =  $-23.5\text{‰}$ , S.D. =  $0.8\text{‰}$ ,  $n = 17$ ). The single black-throated sparrow (*A. bilineata*) caught in 1999 also had a  $\delta^{13}\text{C}$  value consistent with a  $\text{C}_3$ -based diet ( $-25.1\text{‰}$ ), while the Brewer's sparrows (*S. breweri*) caught in 2000, had  $\delta^{13}\text{C}$  values that reflected a  $\text{C}_4$  diet (mean  $\delta^{13}\text{C}$  of bioapatite =  $-8.8\text{‰}$ ). The limited data on these bird species suggested a dietary shift comparable to the majority of rodents (excluding kangaroo rats).

## Discussion

### Oxygen

Results from oxygen isotope analysis provide insight into the physiological and dietary characteristics of the species sampled. Oxygen analysis suggests variation in the water economy and resource selection of the rodents. Kangaroo rats, the largest granivores

and known for their ability to survive on a diet of dry seed using metabolic water alone, had the highest  $\delta^{18}\text{O}$  values. Omnivorous grasshopper mice, presumably obligate drinkers, had the lowest  $\delta^{18}\text{O}$  values, while harvest and pocket mice had intermediate values. The higher  $\delta^{18}\text{O}$  values of the kangaroo rats in relation to those of the harvest mice are probably related to higher water conservation for the former. The low  $\delta^{18}\text{O}$  values for grasshopper mice likely are related to the high frequency of insects in their diet, and resulting high water turnover. A detailed physiological and dietary analysis is necessary to establish a firm understanding of the variation in  $\delta^{18}\text{O}$  among these species. Well-designed laboratory experiments, and additional field samples from a greater variety of species and environmental conditions would help to elucidate the processes that effect oxygen enrichment in the vertebrates at this study site.

As expected, the  $\delta^{18}\text{O}$  values in ectotherms were more enriched than endotherms. This is a likely reflection of differences in diet and water-conservation mechanisms between ectotherms and endotherms (Kohn *et al.* 1996). Earless lizards (*H. maculata*) were a striking exception. The very low  $\delta^{18}\text{O}$  values of *H. maculata* may be the result of some unique dietary or physiological characteristic. *H. maculata* may feed on resources that are tied to ground water, or it may possess a behavioral or physiological characteristic that causes higher body water turnover than other ectotherms. Existing natural history information on *H. maculata* does not describe any unique characteristic that easily explains the low  $\delta^{18}\text{O}$  value.

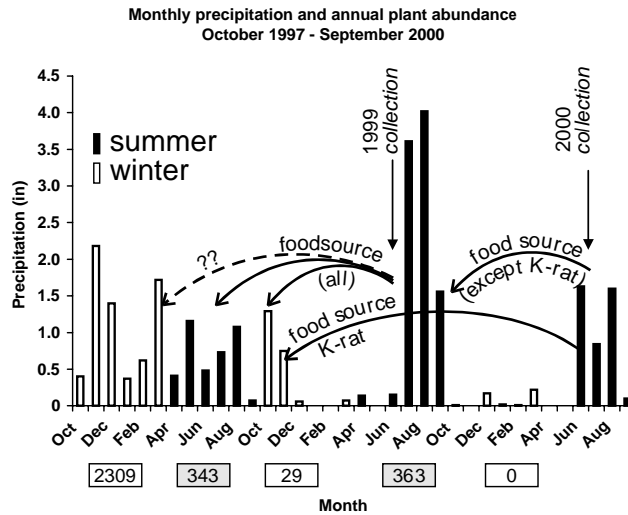
### Carbon

Results from carbon isotope analysis provide preliminary insight into the importance of the limited and seasonal rainfall events, and the different plant photosynthetic pathways of food plants on the diets of the animals. The study site has distinct seasonal rainfall events and plant production:  $\text{C}_3$  annual plants and perennial shrubs use winter rains, while summer rains support predominantly  $\text{C}_4$  annual plants and perennial grasses. Therefore,  $\delta^{13}\text{C}$  values from bone tissue of animals should reflect the proportion of  $\text{C}_3$  and/or  $\text{C}_4$  plants in the diet.

Birds and rodents (excluding kangaroo rats) showed a large, highly significant increase in  $\delta^{13}\text{C}$  values from 1999 to 2000, indicating a change in diet. This reflects plant productivity in the seasons prior to sampling. In response to ample rainfall in the 1997–1998 winter season,  $\text{C}_3$  plant abundance was exceptionally high (>2000 annual stems on unmanipulated control plots, 50 m<sup>2</sup> in size) (Fig. 3). There were fewer  $\text{C}_3$  plants the following winter, with 29 annual stems on control plots (Fig. 3). In 1999, birds and rodents (excluding kangaroo rats) were feeding predominantly on  $\text{C}_3$  plants from the 1998–1999 and perhaps also the 1997–1998 ‘bumper crop’ winter seasons.

In 2000, birds and rodents (excluding kangaroo rats) shifted to a diet of predominantly  $\text{C}_4$  plants. This reflects the heavy summer rains of 1999 and the complete lack of winter  $\text{C}_3$  plant productivity in winter 1999–2000 (Fig. 3). Since the 2000 samples were taken just after the onset of summer rains, the difference between summer bloom and sampling was too short for the 2000 summer signal to be incorporated in the bone structure. Consequently, the  $\delta^{13}\text{C}$  values of birds, grasshopper mice, harvest mice, and pocket mice from 2000 are almost certainly due to the productivity of  $\text{C}_4$  plants from the previous summer. The lack of a  $\text{C}_3$  signal is related to the complete failure of annuals and the lack of  $\text{C}_3$  production during the 1999–2000 winter season.

Kangaroo rats and reptiles, in contrast to grasshopper mice, harvest mice, pocket mice, and birds, maintained  $\delta^{13}\text{C}$  values indicative of a  $\text{C}_3$ -based diet in both 1999 and 2000. This reflects kangaroo rat’s dependence on seed caches from  $\text{C}_3$  plants produced in winter seasons. This result is consistent with the tendency of kangaroo



**Figure 3.** Monthly precipitation and annual plant abundance from October 1997 to September 2000 at the Brown field site. White bars depict winter precipitation (October–March); black bars depict summer precipitation (April–September). White boxes indicate winter annual abundance (number of stems), and shaded boxes indicate summer annual abundance for the season under which they are placed. Annual abundance was determined from quadrant sampling on control plots at the Brown field site. Vertical arrows indicate sample periods. The curved lines indicate presumed food sources for the two sample periods. The kangaroo rats (*D. merriami* and *D. ordii*) were feeding on  $C_3$  plants from the previous one or two winters. In contrast, the non-kangaroo rat rodents (*C. baileyi*, *C. pennellatus*, *O. torridus* and *R. megalotis*) were more opportunistic, feeding on the most abundant food source from the most recent season.

rats to feed selectively on large-seeded plants and to store these seeds for long periods. In addition to the abundance of  $C_3$  annuals produced during the 1997–1998 winter period, and to a lesser extent the 1998–1999 winter periods, seeds from winter annuals are on average twice the mass of summer annual seeds. Results suggest the importance of seed size, abundance, and caching behavior of kangaroo rats, and are consistent with documented differences in resource use between kangaroo rats and other desert rodents (Guo & Brown, 1996).

The  $C_3$ -based diet of reptiles in both 1999 and 2000 may reflect trophic position. Reptiles are primarily insectivorous, and consequently represent a higher trophic level than granivorous rodents. It is possible that resource selection by arthropods is tied to the production of  $C_3$  plants (winter annuals and perennial shrubs), and this signal is passed to lizards through their diet. This result also may imply a lag in the passage of carbon up the food chain.  $\delta^{13}C$  values indicative of a  $C_3$ -based diet in reptiles sampled in 1999 are likely due to winter plant production from the 1997–1998 and 1998–1999 seasons. Given the absence of winter plants in the 1999–2000 season, the diet of reptiles in 2000 may be attributed to  $C_3$  plant production in previous winters.

Results highlight the influence of seasonality, timing and intensity of rainfall events, storage of foods derived from  $C_3$  and  $C_4$  plant selection, water economy, and trophic position on desert animals native to the Chihuahuan Desert. This study describes four important characteristics of the community:

1. Exceptionally high  $\delta^{18}O$  values in most lizards, possibly related to water conservation physiology.

2. Strikingly low  $\delta^{18}\text{O}$  values in earless lizards (*H. maculata*), which cannot be explained in terms of present knowledge of physiological and dietary differences with respect to other lizards.
3. Low  $\delta^{18}\text{O}$  values in omnivorous grasshopper mice (*O. torridus*) compared with that of granivorous rodents, consistent with dietary differences and water economy with respect to granivorous rodents.
4. Exceptionally different temporal patterns of  $\delta^{13}\text{C}$  values in rodents, reflecting differences in  $\text{C}_3$  and  $\text{C}_4$  plants in the diet due to differential reliance of seasonal seed groups and seed stores between kangaroo rats and other granivores.

This study describes a method for tracking seasonal influences, resource availability, dietary shifts, and physiological adaptations in desert vertebrates. It is envisioned that effects of paleoclimatic conditions could be studied by measuring the isotopic compositions of ancient bone material from co-existing kangaroo rats, other rodents, and lizards.

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## Appendix

Sample	Year	$\delta^{13}\text{C}$ (vPDB) Replication						$\delta^{18}\text{O}$ (vSMOW) Replication			
		Bioapatite 1	Diet 1	Bioapatite 2	Diet 2	Diet Mean	Diet S.D.	1	2	Mean	S.D.
<b>Rodents</b>											
<i>D. merriami</i> (Merriam's kangaroo rat)	1999	-15.5	-24.5	-15.7	-24.7	-24.6	0.1	35.7	35.3	35.5	0.3
		-15.9	-24.9	-15.4	-24.4	-24.6	0.3	34.4	32.3	33.4	1.5
		-15.0	-24.0	-15.2	-24.2	-24.1	0.1	33.0	31.7	32.4	0.9
		-13.2	-22.2	-14.7	-23.7	-22.9	1.0	43.6	43.2	43.4	0.3
		-16.7	-25.7	-16.2	-25.2	-25.5	0.4	37.0	36.9	37.0	0.1
		-15.5	-24.5	-15.0	-24.0	-24.2	0.3	34.6	34.8	34.7	0.1
		-17.4	-26.4	-15.1	-24.1	-25.2	1.7	35.6	35.7	35.6	0.0
	2000	-15.5	-24.5	-17.2	-26.2	-25.3	1.2	32.9	33.6	33.3	0.4
		-14.8	-23.8	-17.0	-26.0	-24.9	1.5	32.4	32.7	32.6	0.2
		-19.2	-28.2	-19.1	-28.1	-28.2	0.1	39.2	39.1	39.1	0.0
		-15.0	-24.0	-14.7	-23.7	-23.8	0.2	30.0	32.6	31.3	1.9
		-15.4	-24.4	-15.3	-24.3	-24.4	0.1	31.3	33.3	32.3	1.4
		-16.0	-25.0	-15.9	-24.9	-25.0	0.1	38.0	35.7	36.8	1.7
		-17.2	-26.2	-16.5	-25.5	-25.9	0.5	30.2	31.4	30.9	0.9
<i>D. ordii</i> (Ord's kangaroo rat)	1999	-13.0	-22.0	-12.1	-21.1	-21.5	0.7	42.8	42.1	42.4	0.5
		-14.9	-23.9	-16.5	-25.5	-24.7	1.1	35.7	34.7	35.2	0.7
		-14.5	-23.5	-14.1	-23.1	-23.3	0.3	32.6	31.7	32.1	0.6
		-14.0	-23.0	-14.5	-23.5	-23.2	0.3	33.0	34.3	33.7	0.9
		-15.5	-24.5	-14.9	-23.9	-24.2	0.5	34.5	34.5	34.5	0.0
	2000	-14.7	-23.7	-14.6	-23.6	-23.7	0.1	32.0	32.4	32.2	0.3
		-16.0	-25.0	-17.6	-26.6	-25.8	1.1	33.6	31.6	32.3	1.4
		-16.1	-25.1	-14.4	-23.4	-24.2	1.2	32.7	32.5	32.6	0.1
		-15.4	-24.4	-15.3	-24.3	-24.4	0.1	32.3	33.1	32.7	0.5
		-16.2	-25.2	-16.0	-25.0	-25.1	0.2	25.6	22.5	24.0	2.2
<i>C. baileyi</i> (Bailey's pocket mouse)	1999	-15.4	-24.4	-16.6	-25.6	-25.0	0.8	34.3	34.5	34.4	0.1

		-15.3	-24.3	-15.6	-24.6	-24.5	0.2	31.0	29.6	30.3	1.0
		-16.0	-25.0	-17.1	-26.1	-25.6	0.8	37.4	36.8	37.1	0.4
		-17.2	-26.2	-16.9	-25.9	-26.1	0.2	29.0	27.8	28.4	0.8
	2000	-5.6	-14.6	-4.5	-13.5	-14.1	0.8	30.3	30.7	30.5	0.2
		-5.3	-14.3	-5.4	-14.4	-14.4	0.0	29.1	30.8	30.0	1.3
		-5.6	-14.6	-5.8	-14.8	-14.7	0.1	37.6	37.2	37.4	0.3
		-4.3	-13.3	-3.8	-12.8	-13.0	0.4	39.8	39.8	39.8	0.0
		-9.2	-18.2	-10.6	-19.6	-18.9	1.0	36.5	34.5	35.5	1.4
<i>C. penicillatus</i>	1999	-15.0	-24.0	-15.2	-24.2	-24.1	0.2	28.8	28.7	28.8	0.1
(Desert pocket mouse)		-16.4	-25.4	-16.6	-25.6	-25.5	0.2	32.8	31.9	32.3	0.7
	2000	-8.9	-17.9	-7.2	-16.2	-17.1	1.2	36.4	36.1	36.3	0.2
		-6.0	-15.0	-4.9	-13.9	-14.5	0.8	37.6	36.9	37.3	0.5
		-5.4	-14.4	-6.5	-15.5	-14.9	0.8	23.7	29.9	26.8	4.4
<i>O. torridus</i>	2000	-5.2	-14.2	-5.4	-14.4	-14.3	0.2	30.0	28.6	29.3	1.0
(Northern grasshopper mouse)		-5.6	-14.6	-5.2	-14.2	-14.4	0.3	29.1	29.0	29.1	0.1
		-4.0	-13.0	-4.1	-13.1	-13.0	0.0	30.5	29.9	30.2	0.4
		-4.6	-13.6	-5.4	-14.4	-14.0	0.5	31.3	31.1	31.2	0.1
<i>R. megalotis</i>	1999	-14.7	-23.7	-13.7	-22.7	-23.2	0.7	31.1	30.8	30.9	0.2
(Western harvest mouse)		-14.9	-23.9	-13.4	-22.4	-23.1	1.1	29.4	30.4	29.9	0.7
	2000	-6.3	-15.3	-5.8	-14.8	-15.1	0.4	31.6	30.6	31.1	0.7
		-7.5	-16.5	-7.0	-16.0	-16.2	0.4	39.3	39.1	39.2	0.2
		-0.8	-9.8	-0.7	-9.7	-9.8	0.1	33.7	33.1	33.4	0.5
Reptiles											
<i>H. maculata</i>	1999	-15.6		-15.7				25.9	22.4	24.2	2.5
(Lesser earless lizard)	2000	-14.5		-13.9				26.2	25.0	25.6	0.9
<i>U. ornatus</i>	1999	-14.1		-14.8				45.2	44.4	44.8	0.5
(Northern tree lizard)		-14.1		-15.5				39.7	36.6	38.1	2.2
		-14.3		-14.2				37.6	37.7	37.7	0.1
<i>S. virgatus</i>	1999	-14.6		-14.5				43.7	43.8	43.7	0.0
Striped plateau lizard		-15.4		-15.1				42.0	43.7	42.9	1.2
		-14.7		-14.5				43.6	43.7	43.6	0.0
<i>C. uniparens</i>	1999	-13.0		-14.7				41.3	44.2	42.8	2.1
(Desert grassland whiptail)		-14.0		-15.2				40.1	39.9	40.0	0.1

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Sample	Year	$\delta^{13}\text{C}$ (vPDB) Replication						$\delta^{18}\text{O}$ (vSMOW) Replication			
		Bioapatite	Diet	Bioapatite	Diet	Diet Mean	Diet S.D.	1	2	Mean	S.D.
		1	1	2	2						
<i>S. undulates</i> (Eastern fence lizard)	2000	-15.0		-14.2				41.9	40.2	41.0	1.2
	1999	-15.0		-14.0				39.3	39.6	39.4	0.2
		-15.4		-15.0				38.6	38.6	38.6	0.0
	2000	-14.4		-14.9				38.9	38.5	38.7	0.3
		-13.7		-14.7				38.9	40.4	39.7	1.0
<i>P. melanoleucus</i> (Bull snake)		-14.1		-15.0				38.7	39.3	39.0	0.5
	2000	-11.5		-12.0				43.2	43.0	43.1	0.1
Birds											
<i>A. bilineata</i> (Black-throated sparrow)	1999	-16.3		-15.9				33.6	33.9	33.8	0.2
<i>S. breweri</i> (Brewer's sparrow)	2000	-7.3		-6.8				30.1	30.0	30.1	0.0
		-10.6		-10.5				29.0	29.8	29.4	0.5