

Cacti supply limited nutrients to a desert rodent community

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Abstract In the Sonoran Desert, cacti represent a potentially important source of nutrients and water for consumers. Columnar cacti, in particular, produce a large pulse of flowers and succulent fruit during hot summer months. The importance of cactus stems, flowers and fruit to the small mammal community has not been quantified. We exploited natural variation in the carbon isotope ($\delta^{13}\text{C}$) values of cacti (CAM) versus C_3 plants to quantify the relative use of these resources by a diverse desert small mammal community. We also estimated trophic level by measuring nitrogen isotope ($\delta^{15}\text{N}$) values. We hypothesized that (H_1) granivorous heteromyids (kangaroo rats, pocket mice) would exploit the summer pulse of seeds and pulp; (H_2) folivorous and omnivorous cactus mice, wood rats, and ground squirrels would exploit cacti stems year-round and seeds when available; and (H_3) kangaroo rats and pocket mice would shift from seeds to insects during hot dry months. We found that heteromyids made minimal use of seeds during the period of heavy seed rain. Of the cricetids, only the folivore *Neotoma albigula* made continuous but highly variable use of cacti resources (annual mean = 32 %, range 0–81 %), whereas the omnivore *Peromyscus eremicus* ignored cacti

except during the summer, when it exploited seeds and/or fruit pulp (June–July mean = 39 %, range 20–64 %). We also found little evidence for a shift to greater consumption of insects by heteromyids during the hot dry months. Overall, use of cactus resources by the small mammal community is very limited and highly variable among species.

Keywords $\delta^{13}\text{C}$ · $\delta^{15}\text{N}$ · Sonoran Desert · Stable isotopes · Trophic level

Introduction

Small mammals are successful inhabitants of the hot subtropical deserts of North America. They are abundant, diverse, and able to thrive under environmental conditions that produce significant physiological challenges during much of the year (Schmidt-Nielsen 1964). Nocturnal activity can mitigate some of these challenges, and the importance of this behavioral strategy is evident when one considers that 57 of 61 species (>90 %) of rodents in the Sonoran Desert use this strategy (Walsberg 2000). However, very warm nighttime air temperatures still produce nontrivial challenges for small animals, and under these conditions cacti represent a potentially important source of water and energy. Woody perennials and spring annual species, which use C_3 photosynthesis, represent the bulk of the primary productivity and standing biomass of the Sonoran Desert ecosystem. Nevertheless, in many locations, cacti such as saguaro (*Carnegiea gigantea*), organ pipe (*Stenocereus thurberi*), cholla (*Opuntia* spp.) and desert prickly pear (*O. engelmannii*) can account for a significant portion of overall plant biomass. Desert plants, in general, are known to produce mostly dry fruits and seeds (Bronstein et al. 2007), which contrasts with columnar cacti such as

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saguaro, where the pulp of a single fruit may contain more than 20 ml of water and 90 kJ of energy (Wolf and Martínez del Río 2003). The stems of cacti such as saguaro and organ pipe can be >95 % water by mass and thus store thousands of liters of water on the landscape (Nobel 2002). Although cactus stems contain large quantities of water, their fruits and flowers also present a superabundant seasonal source of carbohydrates and proteins. Saguaro seeds are approximately 50 % of the pulp dry mass and contain 16 % proteins and 30 % lipids by mass, whereas the pulp is composed of only carbohydrates (Wolf and Martínez del Río 2003). In columnar cacti such as *C. gigantea*, the production of thousands of energy-rich flowers and fruit per hectare from May through July releases a large pulse of nutrients (and water) into the community during the hottest and driest period of the year (Wolf and Martínez del Río 2003). As cactus fruits open and dry (June and July), the dried fruits fall from the plant and produce a superabundant but short-lived pulp and seed rain (July and August) that may be an important source of nutrients for rodents and other consumers (Wolf and Martínez del Río 2003).

Although the community structure and foraging ecology of small desert mammals has been studied extensively (Reichman 1975, 1977; Bowers and Brown 1982; Price et al. 2000; Smith et al. 2002), little attention has been focused on the importance of cacti as a source of nutrients for these communities (Vorhies and Taylor 1940; Spencer and Spencer 1941; Olsen 1976). Early observations indicate that some rodents may rely on cacti stems as a source of nutrients (Vorhies and Taylor 1940; Online Resource 1 of the Electronic supplementary material, ESM). From our work on the importance of columnar cacti to the bird community (Wolf and Martínez del Río 2000, 2003; Wolf et al. 2002), and our observations of intense seed rain during periods of peak fruit ripening, we hypothesize that cactus resources (seeds, pulp, and stems) should be used extensively by the rodent community. Although columnar cacti have been considered keystone resources because they provide both water and nutrients to consumers through their flowers and fruits during periods of resource scarcity (Wolf and Martínez del Río 2003), the importance of these and other cacti to the nutritional ecology of the rodent community remains unknown.

This study focuses on quantifying the importance of cacti to the small mammal community. Three families of rodents are common to this hot, subtropical desert ecosystem (Table 1). The most abundant are the Heteromyidae, the kangaroo rats and pocket mice, which in this site vary in size from 5 to 60 g and include *Dipodomys merriami*, *Chaetodipus baiylei*, *Chaetodipus intermedius*, *Chaetodipus penicillatus*, and *Perognathus amplus*. These species are desert-adapted and need little water due to their water-efficient kidneys and gut; they appear to survive cooler

periods on a diet that includes only carbohydrate-rich dry seeds, and they cache large quantities of these resources for later use (Schmidt-Nielsen and Schmidt-Nielsen 1952; Walsberg 2000; Tracy and Walsberg 2002). During the summer, however, some species may include arthropods or green vegetation (Reichman 1975; Hope and Parmenter 2007) in their diets, which contain large amounts of water and protein relative to a dry seed diet. The extent to which these species use cactus resources has never been quantified.

The second group of rodents in the Sonoran Desert belongs to the family Cricetidae, the New World rats and mice, which include *Peromyscus eremicus*, *Onychomys torridus*, and *Neotoma albigula* (15–150 g) at our study sites. These species do not exhibit extensive adaptations to a desert existence (Tracy and Walsberg 2002). Cricetid rodents such as *N. albigula* are known to have higher water requirements, less efficient kidneys, and lower water-use efficiencies than heteromyid rodents (MacMillan and Hinds 1983; Al-kahtani et al. 2004). Measurements of water flux rates in free-living *N. albigula* averaged 20 ml/day in the Chihuahuan Desert of Mexico (Grenot and Serrano 1979), which is 105 % of the estimated water flux based on body mass (Nagy and Peterson 1988). The cactus mouse (*Peromyscus eremicus*) is a small omnivorous mouse that is part of a widespread genus. It feeds on insects, seeds, and green vegetation, and has relatively high water requirements and thus needs to obtain significant free water from its diet (see Table 1). The grasshopper mouse (*Onychomys torridus*) is an omnivore/insectivore that is an aggressive predator and feeds extensively on arthropods, thus obtaining significant free water from its diet. The larger white-throated wood rat (*Neotoma albigula*) is a large folivorous species that eats primarily green vegetation and grazes cactus stems extensively in regions where *Opuntia* cacti are available (Hoffmeister 1986; Online Resource 1 of the ESM). Although observations suggest that *N. albigula* largely specialize on cacti where it is available, the extent to which their diet varies beyond cacti is an open question, and it is unknown how important the abundant seed rain associated with saguaro and organ pipe is for this species.

The third rodent family found in the Sonoran Desert is the Sciuridae, the ground squirrels, of which we captured only the antelope ground squirrel, *Ammospermophilus harrisi*. It is active during the day and is hypothesized to move between deeply shaded bushes, burrows, and sunlit areas to regulate body temperature as it forages (Chappell and Bartholomew 1981). Its diet includes cactus and mesquite seeds, fruit, and occasional arthropods (Best et al. 1990), although the extent of its use of cacti is currently unknown. Despite fairly efficient kidneys, its diurnal activity patterns likely lead to relatively high water requirements, which suggests that it may exploit cactus stems for water.

Table 1 Sonoran Desert rodent species examined in our study listed by taxonomic group

Family	Species	Foraging ecology	Citations	Relative abundance (%)
Cricetidae	<i>Neotoma albigula</i>	Diet: folivorous Seasonality: likely Water efficiency: low	Vorhies and Taylor (1940); Hoffmeister (1986); Dial (1988); Al-kahtani et al. (2004); Dearing et al. (2008)	10.8
	<i>Peromyscus eremicus</i>	Diet: omnivorous Seasonality: high, estivates Water efficiency: low	Hoffmeister (1986); Al-kahtani et al. (2004)	4.3
	<i>Onychomys torridus</i>	Diet: omnivorous/insectivorous Seasonality: low Water efficiency: low	Hoffmeister (1986); Al-kahtani et al. (2004)	0.5
Heteromyidae	<i>Dipodomys merriami</i>	Diet: granivorous Seasonality: low Water efficiency: high	MacMillen and Hinds (1983); Hoffmeister (1986)	17.4
	<i>Chaetodipus baileyi</i>	Diet: granivorous Seasonality: low Water efficiency: high	MacMillen and Hinds (1983); Hoffmeister (1986)	46.8
	<i>Chaetodipus intermedius</i>	Diet: granivorous Seasonality: low Water efficiency: high	MacMillen and Hinds (1983); Hoffmeister (1986)	5.9
	<i>Chaetodipus penicillatus</i>	Diet: granivorous Seasonality: low Water efficiency: high	MacMillen and Hinds (1983); Hoffmeister (1986)	11.2
	<i>Perognathus amplus</i>	Diet: granivorous Seasonality: low Water efficiency: high	MacMillen and Hinds (1983); Hoffmeister (1986)	2.7
Sciuridae	<i>Ammospermophilus harrisi</i>	Diet: folivorous but highly diverse and includes fruits Seasonality: likely Water efficiency: medium	Chappell and Bartholomew (1981); Karasov (1982); Hoffmeister (1986); Best (1990)	0.5

Information regarding general foraging ecology is derived from the listed citations. Relative abundance is calculated as the average percent (for all months) of captures for each species based on total captures; both sites are lumped

In this study, we measure the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values of plant and animal tissues to examine the use of cactus resources by the rodent community. We take advantage of two phenomena to trace the incorporation of cactus nutrients into the rodent community. First, we rely on the observation that $\delta^{13}\text{C}$ values of cacti, which use the CAM photosynthetic pathway, differ greatly from most other plants in the plant community, which use the C_3 photosynthetic pathway. Second, we exploit the predictable patterns between the isotopic composition of consumers' tissues and that of their diet (DeNiro and Epstein 1978; Caut et al. 2009) to estimate the use of cactus resources in rodents and their trophic level by measuring the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of blood samples obtained from the rodent community.

Water is a scarce resource in desert environments. For granivorous rodents, high water requirements may be difficult to meet because seeds are a resource that typically lacks significant free water. For omnivores and herbivores, water may not be in such short supply because

they can exploit cacti. However, the stem tissues of cacti are protected by secondary compounds (e.g., alkaloids and tannins), which limits their use by species not adapted to digest these compounds (Gibson and Nobel 1986). Omnivores may also feed on invertebrates that, similar to cacti, have higher water contents than seeds and leaves. We can quantify seasonal changes in trophic level associated with a shift from plant to insect resource use by measuring $\delta^{15}\text{N}$ values of consumers and their food resources. Values of $\delta^{15}\text{N}$ increase by $\sim 3\text{--}5\text{‰}$ per trophic step and thus are frequently used to assess trophic level (Vanderklift and Pond 2003).

Given the large standing biomass of succulent cactus stems and the seasonal pulse of cactus floral and fruit resources, we examined three non-mutually exclusive hypotheses pertaining to the use of cactus resources by the rodent community in the Sonoran Desert. The first hypothesis (H_1) proposes that granivorous heteromyid rodents, such as kangaroo rats and pocket mice, will forage on the seed rain associated with the fruiting of saguaro and organ

pipe cacti because it is an easily exploited and seasonally abundant source of energy and nutrients. Under this scenario, we predict that heteromyid plasma $\delta^{13}\text{C}$ values will be higher during the peak period of cacti fruit and seed availability (July–August) in comparison to other periods of the year, when C_3 resources likely dominate their diets.

The second hypothesis (H_2) posits that cactus mice, wood rats, and ground squirrels will consume cactus stems throughout the year to meet their water and energy requirements, and also extensively use the seasonal pulse of cacti fruit during the summer. Because of their greater water demands and less efficient kidneys (MacMillen and Hinds 1983; Al-kahtani et al. 2004), these species may use cacti as both a nutrient and a water resource, thus taking advantage of this seasonally abundant resource during a period of the year when other food and water resources are scarce. Under this scenario, we predict that these species would have consistently elevated plasma $\delta^{13}\text{C}$ values throughout the year, indicating use of both the seasonal fruit/seed rain in the summer months and cactus stems during other periods of the annual cycle.

Finally, our third hypothesis (H_3) proposes that kangaroo rats and pocket mice may shift to eating arthropods, which have high water contents relative to seeds, during the hotter and/or dryer periods of the year (May–November) to obtain the water needed to maintain osmoregulatory homeostasis. This upward shift in trophic level during the hottest and driest months would be indicated by increases in $\delta^{15}\text{N}$ values of rodent plasma during this period. Consistent with H_2 , we did not expect to observe trophic level shifts in wood rats because of their ability to digest secondary compounds found in cactus stems that are available year round (Dearing et al. 2000; Sorensen et al. 2004; Pichersky and Lewinsohn 2011).

Materials and methods

Study site

Fieldwork was conducted in 2005–2006 at Organ Pipe Cactus National Monument, Arizona (N32°05.506', W112°46.146') located 214 km southwest of Tucson, Arizona, United States. The plant community is classified as Arizona upland or saguaro/paloverde forest (Shreve and Wiggins 1965). This area is characterized by the presence of columnar cacti, leguminous trees, and bi-modal precipitation. We sampled two nearby sites (5 km apart), which we will refer to as the Uplands and Flats sites. The Uplands site comprised a sloping rocky substrate containing many large boulders and rocks with variable elevation (700–853 m above sea level) and an average density of columnar cacti of 20 plants/ha in relative proportions of ~15 *C.*

gigantea and ~5 *Stenocereus thurberi*. Located 5 km to the west, the Flats site was named for its consistently low elevation (610–660 m above sea level). The substrate at the Flats was soft sand with very few rocks or boulders. Precipitation at both sites was very low (average of 17 mm/month), with a maximum rainfall in August in both years of the study (360–880 mm), and no precipitation documented from November to February, nor in May.

Field procedures

Walking surveys were conducted monthly to assess the phenology of the plant community and estimate the productivity of columnar cacti. This was done over an area that included both the trapping grids and transects used to sample the rodent community. We counted the number of cacti and recorded species, reproductive stages, and counts of both flowers and fruit at 10-m intervals along trapping transects. All cacti within 15 m of the transect line were included, and species and height were recorded. Additional plant sampling was done by overlaying 20 × 5 m plots on the trapping transects with 20-m gaps between each plant transect. Plant plot centers coincided with transect trap stations. Plant material was collected from several individuals of each plant species from both trapping locations for stable isotope analysis (Table 2).

We trapped live rodents monthly with Sherman traps (8 cm × 10 cm × 31 cm) from May 2005 through September 2006. Total trapping effort included 3277 trap nights spread over 36 nights for an average of 2 days of trapping per month. This research was conducted with the approval of the University of New Mexico (UNM) Institutional Animal Care and Use Committee (05MCC005), under permits from Organ Pipe Cactus National Monument and Arizona Department of Game and Fish (SP640534). Both grids and transects were used to sample the rodent community at each site, and 130 traps were used each night. Traps in the grids were set up as a square with all traps spaced 10 m apart from neighboring traps in either direction and as 10 m apart as paired trap stations in transects. Grids were set up in a 5 trap × 5 trap arrangement, resulting in a total of 25 traps per grid. A paired-trap transect, in addition to a grid on each site, allowed the capture of more rodent species by covering a wider array of microhabitats (40 traps total = 2 traps at each of the 20 stations). Traps were opened in the evening before sunset and checked at dawn, and animals were returned to their original trapping locations after processing. For small rodents (<60 g), handling time was kept under 10 min for each individual and followed the American Society of Mammalogists Guidelines (American Society of Mammalogists Animal Care and Use Committee 1998). To prevent injury during bleeding, animals larger than 100 g were sedated during processing using isoflurane

Table 2 Mean (\pm SD) and ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the dominant plants collected at our sites in Organ Pipe Cactus National Monument during 2005 and 2006

	Species	Common name	Tissue	N	Mean $\delta^{13}\text{C}$ (\pm SD)	$\delta^{13}\text{C}$ range	Mean $\delta^{15}\text{N}$ (\pm SD)	$\delta^{15}\text{N}$ range
CAM	<i>Carnegieia gigantea</i>	Saguaro	Seeds	5	-13.8 ± 0.4	-13.3/-14.3	5.9 ± 2.2	3.4/7.6
	<i>Carnegieia gigantea</i>	Saguaro	Fruit	4	-12.7 ± 0.2	-12.5/-13.0	3.9 ± 2.3	1.5/6.3
	<i>Cylindropuntia fulgida</i>	Chain fruit cholla	Fruit	5	-13.4 ± 0.2	-13.1/-13.7	3.7 ± 1.0	3.6/4.9
	<i>Cylindropuntia fulgida</i>	Chain fruit cholla	Plant pulp	5	-13.7 ± 0.8	-12.8/-14.8	3.9 ± 0.7	3.5/5.3
	<i>Echinocereus</i> sp.	Hedgehog cactus	Plant pulp	3	-11.4 ± 0.4	-11.0/-11.7	3.5 ± 1.4	2.2/5.0
	<i>Opuntia</i> sp.	Prickly pear cactus	Plant pulp	5	-12.7 ± 0.8	-11.9/-13.6	5.9 ± 0.9	5.2/7.4
	<i>Opuntia versicolor</i>	Staghorn cholla	Plant pulp	3	-12.9 ± 0.9	-12.2/-14.0	6.8 ± 5.1	2.2/12.4
	<i>Stenocereus thurberi</i>	Organ pipe cactus	Seeds	5	-12.5 ± 0.4	-12.0/-13.1	6.3 ± 0.9	5.6/7.9
	<i>Stenocereus thurberi</i>	Organ pipe cactus	Fruit	7	-11.8 ± 0.3	-11.6/-12.2	5.3 ± 1.2	3.5/6.5
	C ₃	<i>Acacia greggii</i>	Catclaw acacia	Leaves and seeds	5	-27.0 ± 1.3	-25.3/-28.8	6.5 ± 0.9
<i>Ambrosia deltoidea</i>		Triangle bursage	Leaves and seeds	5	-26.2 ± 1.7	-25.2/-26.9	4.8 ± 0.6	7.0/11.4
<i>Ambrosia dumosa</i>		White bursage	Leaves and seeds	4	-24.9 ± 0.2	-24.6/-28.8	4.8 ± 1.3	3.9/6.2
<i>Celtis pallida</i>		Desert hackberry	Leaves and seeds	5	-25.2 ± 1.1	-23.6/-26.5	8.8 ± 1.9	5.6/10.5
<i>Cercidium microphyllum</i>		Yellow paloverde	Leaves and seeds	5	-24.5 ± 0.8	-23.7/-24.9	5.3 ± 0.5	4.7/5.9
<i>Cordylanthus parviflorus</i>		Birds beak	Leaves and seeds	3	-25.0 ± 0.8	-24.3/-25.9	3.1 ± 1.2	2.5/4.8
<i>Coursetia glandulosa</i>		Rosary babybonnets	Leaves and seeds	4	-24.9 ± 0.6	-24.5/-25.8	2.6 ± 1.5	1.4/4.6
<i>Cryptantha</i> sp.		Borage	Leaves and seeds	5	-27.2 ± 1.6	-25.3/-29.4	5.5 ± 0.9	4.5/6.5
<i>Encelia farinose</i>		Brittlebush	Leaves and seeds	5	-25.2 ± 0.8	-24.1/-25.9	6.9 ± 0.7	6.0/7.7
<i>Fouquieria splendens</i>		Ocotillo	Leaves	4	-23.9 ± 1.2	-22.1/-24.9	3.7 ± 0.6	3.1/4.5
<i>Hibiscus coulteri</i>		Desert rosemallow	Leaves and seeds	3	-27.2 ± 0.3	-26.8/-27.4	4.0 ± 0.4	3.6/4.4
<i>Janusia gracilis</i>		Slender janusia	Leaves and seeds	4	-26.1 ± 0.5	-25.4/-26.4	6.7 ± 1.0	6.5/8.5
<i>Jatropha cardiophylla</i>		Limberbush	Leaves and seeds	5	-25.4 ± 0.6	-24.6/-25.9	4.1 ± 0.5	3.5/4.7
<i>Larrea tridentata</i>		Creosote	Leaves and seeds	5	-23.4 ± 0.5	-22.2/-23.9	5.8 ± 0.9	4.2/5.5
<i>Malvaceae</i> sp.		Mallow	Leaves and seeds	4	-27.2 ± 1.5	-25.2/-28.7	5.9 ± 0.8	5.5/7.1
<i>Olneya tesota</i>		Olneya	Leaves and seeds	5	-24.6 ± 0.4	-24.1/-25.0	5.6 ± 1.1	3.9/6.6
<i>Phoradendrum californicum</i>		Mistletoe	Stems	2	-26.2 ± 0.7	-25.7/-26.6	3.6 ± 1.1	2.8/4.4
<i>Phoradendrum californicum</i>		Mistletoe	Leaves	2	-24.6 ± 1.4	-23.6/-25.7	1.8 ± 0.3	1.5/2.2
<i>Phoradendrum californicum</i>		Mistletoe	Fruit	2	-25.4 ± 0.9	-24.7/-26.0	3.9 ± 0.3	3.8/4.2
<i>Prosopis velutina</i>		Velvet mesquite	Leaves and seeds	3	-24.3 ± 1.3	-23.2/-25.6	2.3 ± 1.4	1.0/3.7
<i>Sapium biloculare</i>		Mexican jumping bean	Leaves and seeds	4	-23.9 ± 1.2	-23.9/-24.9	2.5 ± 0.6	3.1/4.5
<i>Simmondsia chinensis</i>		Jojoba	Leaves and seeds	5	-26.1 ± 1.1	-24.8/-26.8	4.3 ± 1.5	2.6/6.3
<i>Sphaeralceae ambigua</i>		Globemallow	Leaves and seeds	3	-27.7 ± 0.4	-27.2/-27.9	5.1 ± 0.8	4.8/5.5
<i>Vulpia octoflora</i>		Six-weeks fescue	Leaves and seeds	2	-25.9 ± 0.2	-25.8/-26.1	2.0 ± 1.0	1.3/2.8

and a portable anesthesia machine (Online Resource 3 in the ESM).

Plasma samples were used to estimate resource use via stable isotope analysis. This is because plasma exhibits fast isotopic incorporation rates; half lives ($t_{1/2}$) for endotherms are 2–3 days, which equates to complete turnover in ~2–3 weeks (Hobson and Clark 1992; Pearson et al. 2003; Martínez del Rio et al. 2009). Thus, plasma provides insight into the resources the animal has been using within a period that is short enough to quantify monthly shifts in resource use by small mammals associated with seasonal changes in resource abundance (C₃ plants and cacti). Resources typical of this environment (seeds and insects) have modest lipid

contents, and the large difference of >12‰ in $\delta^{13}\text{C}$ values between C₃ and cactus resource end members makes variation in lipid content of plasma a minor issue (Post et al. 2007).

A 50- μL blood sample was obtained by slipping a heparinized microcapillary tube (heparinized 50- μL capillary tubes; Fisher, Pittsburgh, PA, USA) behind the eye to puncture the retro-orbital sinus (Heteromyidae) or super-orbital sinus (Cricetidae, Sciuridae). Before bleeding, a drop of local anesthetic (a sterile ophthalmic solution, Tetracaine Hydrochloride Ophthalmic Solution, USP, 0.5 %) was applied to the eyes of all animals. Excess solution was removed by gently blotting the area so that the anesthetic

would not affect the isotopic composition of plasma samples. Blood was prepared for stable isotope analysis via centrifugation within 12 h of collection. Blood was spun for 3 min in a centrifuge (IEC MB centrifuge microhematocrit, Thermo Scientific, Waltham, MA, USA) to separate erythrocytes from plasma.

Stable isotope analyses

Approximately 15 μl of plasma were pipetted into pre-cleaned 5×3.5 mm tin capsules (Alpha Resources Inc., Stevensville, MI, USA) and placed in a drying oven overnight prior to isotope analysis; a single sample was analyzed for each individual. Plant materials were dried and ground into a fine powder. Plant material (3–5 mg) was loaded into tin capsules for carbon and nitrogen isotope ratio measurements. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values were measured using an ECS 4010 elemental analyzer (Costech Analytical Technologies, Valencia, CA, USA) coupled to a Thermo Finnigan (Waltham, MA, USA) Delta Plus continuous flow mass spectrometer in the UNM Department of Earth and Planetary Sciences. Stable isotope values are reported using delta (δ) notation in parts per mil (‰) as: $\delta \text{‰} = (R_{\text{sample}}/R_{\text{standard}}) \times 1000$. R_{sample} and R_{standard} are the relative ratios of the heavy and light isotopes ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) in a sample and standard, respectively. Isotope values are referenced against international standards of Vienna Pee-Dee Belemnite (VPDB) for carbon and air for nitrogen. Measured isotope values were calibrated against international standards using internal reference materials (valine and sorghum flour) that were run alongside plasma and plant material samples to correct for instrument drift. Repeated within-run measurement of these reference materials yielded an analytical precision (SD) of 0.1 ‰ for $\delta^{13}\text{C}$ and 0.2 ‰ for $\delta^{15}\text{N}$. Reference materials were carefully weighed so that they contained similar amounts of carbon and nitrogen to the unknown (plasma or plant material) samples to minimize the effects of nonlinearity on measured isotopic composition.

Estimation of cactus use

Previous work in the Sonoran Desert has shown that cacti tissues have higher $\delta^{13}\text{C}$ values by an average of 13 ‰ compared to those of C_3 plants (Wolf and Martínez del Río 2000). We exploited this difference and used a two-source, one-isotope Bayesian mixing model, Stable Isotope Analysis in R or SIAR (Parnell et al. 2010), to estimate the proportion of a rodent's assimilated carbon that was derived from cacti. Mean (\pm SD) $\delta^{13}\text{C}$ values for C_3 plants and cactus end members used in the model were derived from plant samples collected from our field sites; cactus ($N = 6$ species, $N = 42$ individual samples): -12.8 ± 0.8 ‰; C_3 plants ($N = 28$ species, $N = 105$ individual samples): -25.7 ± 1.1 ‰. We

estimated a $\delta^{13}\text{C}$ trophic discrimination factor ($\Delta^{13}\text{C}_{\text{tissue-diet}}$) for rodents by comparing plasma $\delta^{13}\text{C}$ values to that of C_3 plants collected during the spring, when these plant resources dominate the diets of most rodent species. The difference between the $\delta^{13}\text{C}$ of rodent plasma and the mean $\delta^{13}\text{C}$ value of C_3 plants in the spring provided an apparent discrimination factor ($\delta^{13}\text{C}_{\text{plasma-plant}}$), which we used as the trophic discrimination factor in SIAR. The mean (\pm SD) apparent discrimination factor varied between 3.2 ± 0.5 ‰ (*Dipodomys merriami*, *Chaetodipus intermedius*, and *Chaetodipus penicillatus*) to 3.6 ± 1.1 ‰ (*Chaetodipus baileyi*, *Peromyscus eremicus*). We estimated the standard deviation of this apparent discrimination factor to be 0.5 ‰ in SIAR. We have found similar apparent discrimination factors (3.3 ‰) for bird communities in Sonoran Desert ecosystems (Wolf and Martínez del Río 2003). Furthermore, given the large $\delta^{13}\text{C}$ difference (10–12 ‰) between the two compartments (CAM and C_3 plants) of primary production in this ecosystem, relatively small errors in our discrimination factor do not alter our conclusions regarding the importance of cacti to the various species of small mammals analyzed in our study. Lastly, we used the SIAR package Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2011) to quantify isotope variation at the species level as measured by standard ellipse areas in $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ bivariate space (Fig. 3); ellipse areas are reported in units of ‰².

Estimation of trophic level

Comparison of plasma $\delta^{15}\text{N}$ values among rodent species allowed us to evaluate relative trophic level (DeNiro and Epstein 1981; Kelly 2000). We did not use equations (e.g., Post et al. 2002) that compare the $\delta^{15}\text{N}$ value of the base of the food web (plants) to that of consumers (rodents) to estimate trophic level given the high degree of variation in plant $\delta^{15}\text{N}$ values at our site (Table 2). Thus, our analyses examine raw $\delta^{15}\text{N}$ values between and among species. All statistics were conducted in SPSS (version 11.5 for Windows). Plasma $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and mixing-model output (reported as percent CAM) were each examined by month, species, sex, and site using ANOVAs and ANCOVAs. Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among rodent species and plant functional groups (C_3 versus CAM) were assessed using a MANOVA and Bonferroni post hoc tests to adjust for multiple comparisons.

Results

Abundance and phenology of cacti

Carnegiea gigantea were more abundant at the Flats (64 plants/ha) versus the Uplands (18 plants/ha) site, and

S. thurberi were only found at the Uplands site. Other cacti at the Upland site included *O. fulgida* (~5 plants/ha) and both *O. engelmannii* and *Ferocactus* sp. (<2 plants/ha); these noncolumnar cacti accounted for around 2 % of total plant cover. Overall, cacti at the Uplands site accounted for approximately 27 % of total plant cover. The (C₃) woody plant community on the Upland site was dominated by *Simmondsia chinensis* and *Encelia farinosa*. The sandy Flats site was dominated by woody plants, including *Larrea tridentata* and *Fouquieria splendens*. Overall, cacti accounted for approximately 15 % of the total plant cover at the Flats site.

Both *C. gigantea* and *S. thurberi* bloomed from May to June, with fruits gradually ripening in June. Ripe fruits were available until August, at which point all the fruits had been removed directly from cacti or from the ground, where they had fallen as seed rain earlier in the summer. Peak fruit availability occurred in July, and seed rain occurred from July until August. *C. gigantea* and *S. thurberi* seeds were unavailable during the rest of the year as an income resource to the community, as they were no longer available from plants and the surrounding area after this massive but short-lived influx of seeds and fruit. Other cacti included the relatively abundant *O. fulgida*, which occurred at both sites and bloomed in July. In contrast to *C. gigantea* and *S. thurberi*, *O. fulgida* fruits remain on plants throughout the year and thus were available to consumers in all months. *Cylindropuntia arbuscula* were only noted on the Flats, and bore medium-sized fruit in July. Smaller cacti, *Ferocactus* sp. and *Mammillaria grahamii*, were found at both sites and provided small fruits in late summer through early fall. As previously documented (Wolf and Martínez del Río 2000), $\delta^{13}\text{C}$ values of plants varied by functional group, with CAM and C₃ plants having mean $\delta^{13}\text{C}$ values of -12.8 ± 0.8 and -25.7 ± 1.1 ‰, respectively (Table 2). Mean $\delta^{15}\text{N}$ values for CAM and C₃ plants were 5.1 ± 2.0 and 5.0 ± 2.3 ‰, respectively. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and associated standard deviations for individual species are presented in Table 2.

Rodent abundance

The most abundant rodent was *Chaetodipus baileyi*, and the least was *Onychomys torridus* (Table 1). *Ammospermophilus harrisi* was poorly represented in our sample because it is a diurnal rodent and was not targeted in our trapping efforts. For the focal nocturnal rodent community, species abundance and diversity of rodents changed seasonally, and smaller heteromyids were conspicuously absent from captures during winter months. *Chaetodipus baileyi* was the most abundant heteromyid, and *Perognathus amplus* the least. Larger species were captured year-round (*Dipodomys merriami*, *C. baileyi*). Mid-sized rodents such as *C.*

intermedius and *C. penicillatus* were captured fairly regularly. However, the similarly sized *Peromyscus eremicus* was captured only occasionally during the summer months.

Interactions between species, month, and site: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

A MANOVA assessing both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values revealed a significant month by species interaction ($F_{118,812} = 1.401$, $p = 0.004$). This effect was primarily driven by $\delta^{13}\text{C}$ ($F_{59,812} = 1.535$, $p = 0.008$) and not $\delta^{15}\text{N}$ ($F_{59,812} = 1.255$, $p = 0.102$; MANOVA between-subjects effects).

Species was a significant predictor of $\delta^{13}\text{C}$ (ANOVA $F_{8,826} = 58.154$, $p < 0.001$) and $\delta^{15}\text{N}$ values (ANOVA $F_{8,805} = 18.369$, $p < 0.001$). Furthermore, utilization of cactus materials differed among species, as indicated by Bonferroni post hoc tests (Fig. 1). A MANOVA of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for all individuals revealed that month was a significant predictor of both variables ($F_{20,812} = 11.133$, $p < 0.001$). We also noted a species by site interaction for both isotopes (MANOVA $F_{4,812} = 7.016$, $p < 0.001$). Differences were seen in cactus use among the Upland and Flats sites only in *C. baileyi* ($t_{270} = 16.013$, $p < 0.001$, t test). *Chaetodipus baileyi* also exhibited a highly variable diet both at the Flats and at the Uplands compared to other species (Figs. 1, 2b). We found significant differences in plasma $\delta^{13}\text{C}$ between the sites (ANOVA $F_{1,833} = 3.986$, $p = 0.046$) but not between the sexes (ANOVA $F_{1,833} = 0.006$, $p = 0.939$). In contrast, $\delta^{15}\text{N}$ values did not differ significantly between sites (ANOVA $F_{1,812} = 0.149$, $p = 0.699$) or between the sexes (ANOVA $F_{1,812} = 0.052$, $p = 0.820$). MANOVA results for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ revealed that neither site ($F_{2,619} = 1.882$, $p = 0.153$) nor sex ($F_{2,619} = 0.028$, $p = 0.972$) were significant factors when these two isotopes were considered simultaneously.

Cactus use by rodents: mixing model results

Cacti supplied only limited resources to most heteromyid rodents. For *Dipodomys merriami*, *Chaetodipus baileyi*, *C. intermedius*, *C. penicillatus*, and *Perognathus amplus*, cactus resources accounted for <10 % of their annual total incorporated carbon (Figs. 1, 2a–g, and Table 3). Use of cactus resources by these species typically peaked in July and August during the period of intense seed rain, as well as when it is hottest and driest at the site. During this period, cactus resources accounted for a significant portion on the incorporated carbon in *C. baileyi* (mean = 29.4 ± 14.9 % SD), *C. intermedius* (mean = 22.3 ± 14.9 %), *C. penicillatus* (mean = 16.0 ± 13.4 %), and *P. amplus* [mean = 36.7 % ($N = 1$)] (Table 3; Fig. 1).

Relative to heteromyids, cactus resources were more important to some cricetid and sciurid rodents in the

community. *Neotoma albigula* showed the greatest use of cactus resources (mean = 53.9 ± 23.7 %; Fig. 1), with maximum use occurring during July (55.0 ± 20.9 %, Fig. 2f). *Peromyscus eremicus* showed modest use of cactus resources on an annual basis (mean = 8.0 ± 12.4 %; Fig. 1) but intense use in July during the period of fruiting and seed rain (47.2 ± 12.9 %; Fig. 2g). Limited data for *Onychomys torridus* ($N = 6$) indicate that cactus resources may be of some importance, with a mean annual cactus use of 14.2 % (Fig. 1) and a peak in use of 37.7 % in July. The sciurid *Ammospermophilus harrisi* was the only diurnal rodent captured, and it showed extensive use of cactus resources (annual mean = 51.5 ± 20.5 %, Fig. 1; Table 3), with a peak use of 77.6 % in March before the summer fruiting period, suggesting extensive use of cactus stems.

Dietary variation: standard ellipse areas

$\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ bivariate plots and associated standard area ellipses (Fig. 3) show varying levels of cacti use by the small mammal community during summer (fruit ripening) versus the rest of the year. There was a good deal of overlap between the summer and fall-winter-spring ellipses for the heteromyid rodents *Dipodomys merriami* and *Perognathus amplus*. The relative position of the ellipses in bivariate space suggested little use of cacti in the summer months. Ellipses for the three *Chaetodipus* species were generally larger than for *Dipodomys* or *Perognathus*,

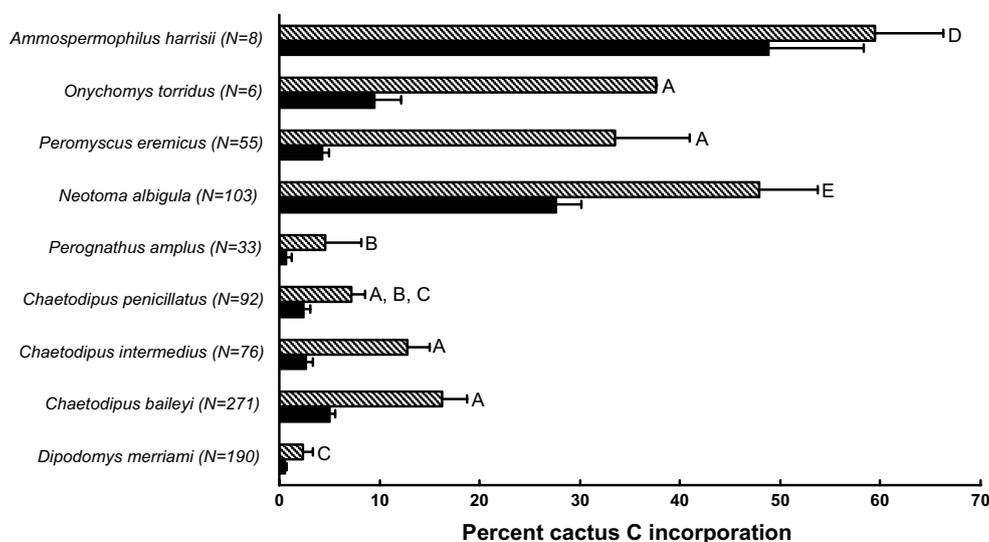


Fig. 1 Mean cactus carbon incorporation by species as estimated from plasma $\delta^{13}\text{C}$ measurements and a two end-member mixing model. Average dietary cactus incorporation outside of peak cactus fruit and seed availability (all individuals, September–June) is illustrated as a percentage by the solid black bars. Hatched bars indicate relative cactus incorporation during periods of maximum cactus fruit and seed availability (July and August). Error bars indicate

Fig. 2 Monthly changes in plasma $\delta^{13}\text{C}$ and percent cactus carbon incorporation in heteromyid rodents (a *Dipodomys merriami*, b *Chaetodipus baileyi*, c *Chaetodipus intermedius*, d *Chaetodipus penicillatus*, e *Perognathus amplus*, f *Neotoma albigula*, g *Peromyscus eremicus*); data from both sites (Uplands and Flats) were combined. Horizontal gray bars indicate the period of cactus fruit availability and thus periods during which we predicted heteromyid rodents would utilize cacti seeds (re: seasonal importance of cacti to granivores, as hypothesized in H₁). Black circles indicate single individual measurements during 2005 and 2006. Percent cactus incorporation (right-side y-axis) was estimated using a linear mixing model with mean cactus $\delta^{13}\text{C} = -12.8$ ‰ VPDB and C₃ plant $\delta^{13}\text{C} = -25.7$ ‰ VPDB as end-member values; see “Methods” for more information about mixing model assumptions. Values below the zero line for cactus incorporation represent animals that did not consume cacti

suggesting a higher degree of dietary generalism for members of this genus relative to other heteromyids, especially during the summer. Many *Chaetodipus* individuals sampled during the summer had high $\delta^{13}\text{C}$ values, indicative of cacti consumption (Fig. 3a–c). For example, the area of the ellipse for *C. baileyi* was large (>5 ‰²) in both seasons (Fig. 3b), but the summer ellipse was larger than that for winter because many individuals had high $\delta^{13}\text{C}$ values associated with the use of cactus. The cricetid *Neotoma albigula* also had large ellipses (~ 7 ‰²), and this was the only rodent species that consumed high proportions of cactus in both the winter and summer seasons (Fig. 3f). Furthermore, there was little overlap between winter and summer ellipses for *N. albigula*, suggesting that this

standard deviations. ANCOVA species differences were significant ($p < 0.001$). Results from ad hoc Bonferroni tests examining differences between species pairs are indicated by letters. Shared letters indicate no significant differences between species using an α -level of 0.05. These tests were applied to data for each species with all months and sites combined

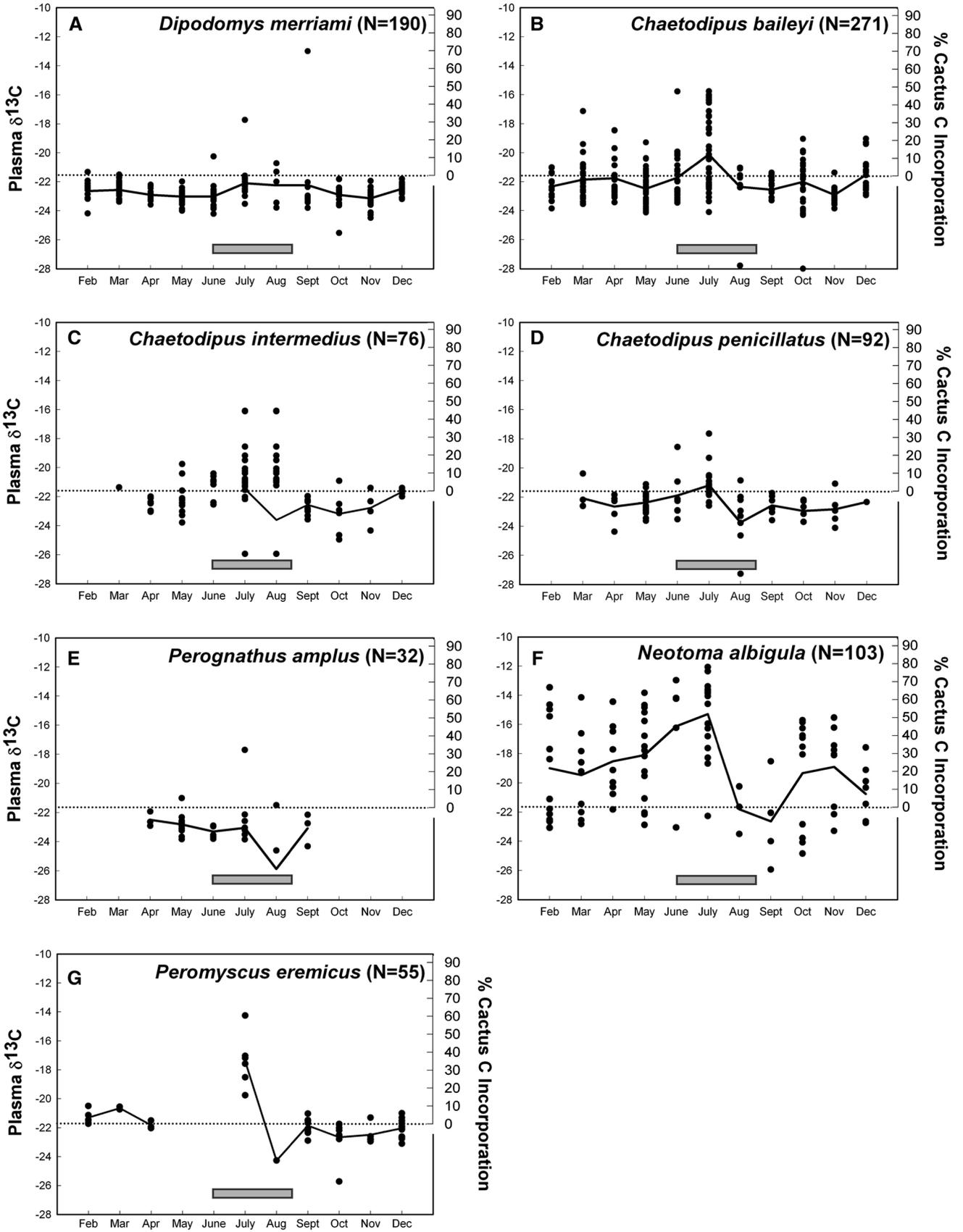


Table 3 Mean (\pm SD) plasma $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for rodents captured at our sites in Organ Pipe Cactus National Monument during 2005 and 2006

Family	Species	Site	N $\delta^{13}\text{C}$ ($\delta^{15}\text{N}$)	Mean $\delta^{13}\text{C}$ \pm SD	$\delta^{13}\text{C}$ range	Cactus use % \pm SD	Mean $\delta^{15}\text{N}$ \pm SD	$\delta^{15}\text{N}$ range
Cricetidae	<i>Neotoma albigula</i>	Flats	26	-16.5 ± 1.9	$-12.3/-20.3$	46.3 ± 15.0	9.3 ± 0.2	7.3/10.3
		Uplands	77 (75)	-19.2 ± 3.5	$-12.0/-25.9$	26.6 ± 25.6	8.7 ± 0.7	7.0/ 10.3
	<i>Peromyscus eremicus</i>	Flats	1	-21.5	NA	6.9	9.9	NA
Heteromyidae	<i>Onychomys torridus</i>	Uplands	54	-21.8 ± 1.8	$-14.3/-25.7$	8.8 ± 13.6	10.3 ± 0.9	7.2/12.0
		Flats	6	-20.7 ± 1.7	$-17.6/-22.8$	14.0 ± 5.2	11.5 ± 0.5	10.7/11.9
	<i>Dipodomys merriami</i>	Flats	190 (185)	-22.8 ± 0.8	$-17.7/-25.5$	1.0 ± 3.4	9.1 ± 0.8	6.2/10.9
		Uplands	132 (130)	-22.7 ± 1.2	$-20.1/-29.6$	2.0 ± 3.6	9.1 ± 0.8	6.9/10.9
	<i>Chaetodipus baileyi</i>	Uplands	132 (130)	-20.9 ± 1.9	$-15.8/-24.1$	13.0 ± 13.6	8.8 ± 1.5	3.9/12.9
		Flats	20 (19)	-22.8 ± 0.8	$-21.3/-24.9$	0.9 ± 2.4	8.8 ± 0.8	7.5/9.9
	<i>Chaetodipus intermedius</i>	Uplands	56 (54)	-21.6 ± 1.8	$-16.1/-27.2$	8.8 ± 2.4	9.3 ± 1.2	5.1/11.4
		Flats	73 (71)	-22.5 ± 1.3	$-17.6/-28.3$	2.9 ± 5.3	8.8 ± 0.7	6.9/10.4
	<i>Chaetodipus penicillatus</i>	Uplands	20 (18)	-21.6 ± 1.3	$-18.6/-23.6$	7.9 ± 8.6	8.5 ± 1.9	5.4/12.2
		Flats	33 (32)	-23.1 ± 1.9	$-17.7/-31.5$	2.0 ± 1.0	8.6 ± 0.8	6.4/9.9
Sciuridae	<i>Perognathus amplus</i>	Flats	5	-16.7 ± 2.6	$-13.9/-20.3$	44.4 ± 20.3	7.8 ± 0.6	7.1/8.2
		Uplands	3	-14.3 ± 2.3	$-12.5/-16.8$	63.3 ± 17.8	8.2 ± 1.1	7.3/9.9

Also shown are estimates of cactus use based on mixing model output (see “Methods”). For species that were captured at both sites (Flats and Uplands), we present mean values for both sites. If only one site is listed, the species was only captured at that site. Sample sizes are listed in relation to $\delta^{13}\text{C}$; if the sample size was different for $\delta^{15}\text{N}$, that sample size is given in parentheses

species is a cactus specialist in the summer months. Lastly, the cricetid *Peromyscus eremicus* also showed a large $\delta^{13}\text{C}$ shift suggestive of cactus consumption during the summer months, with little overlap between winter and summer ellipses (Fig. 3g), but note the relatively small sample size for this species in summer ($N = 6$) versus winter ($N = 49$).

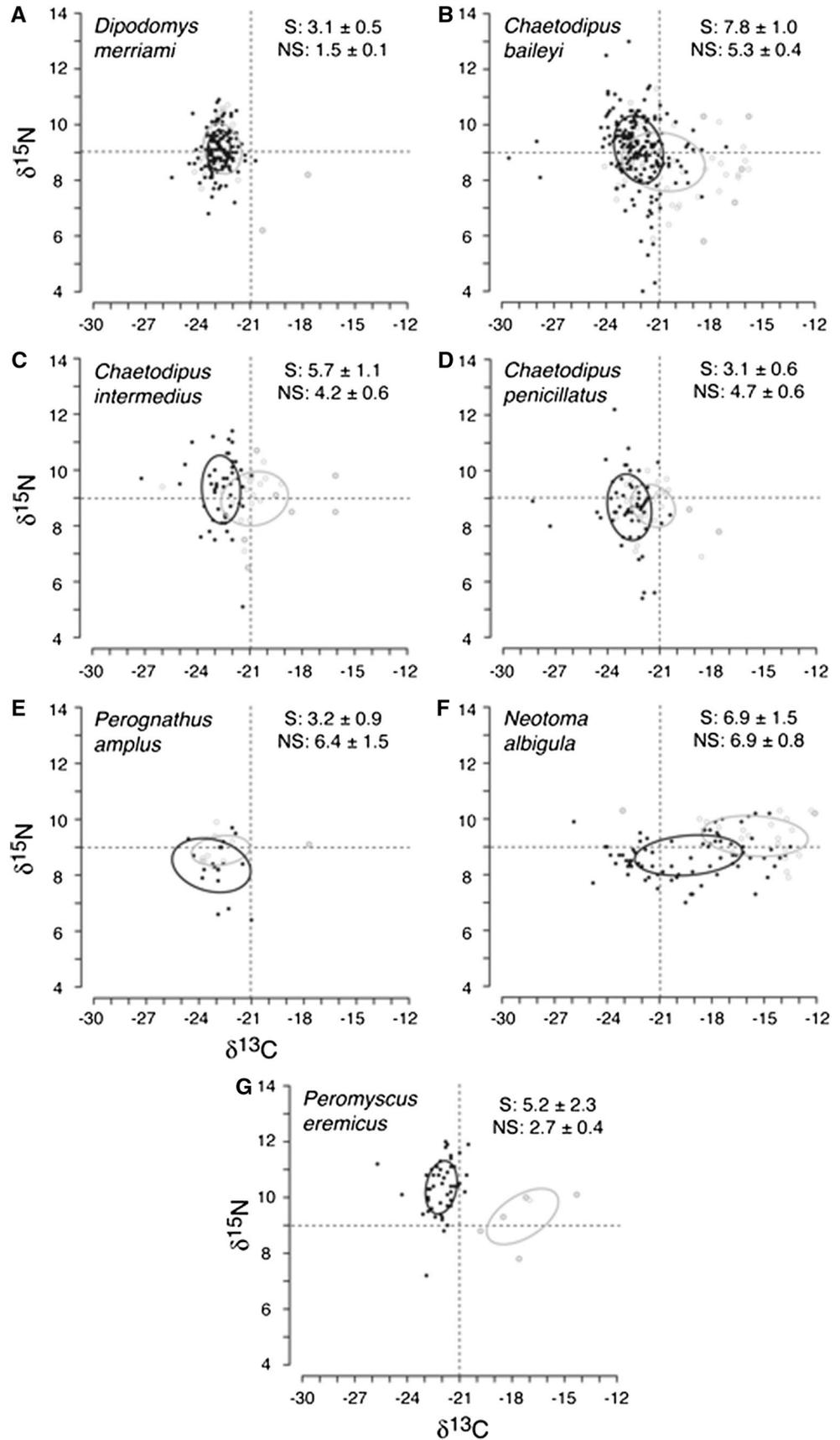
Rodent trophic level

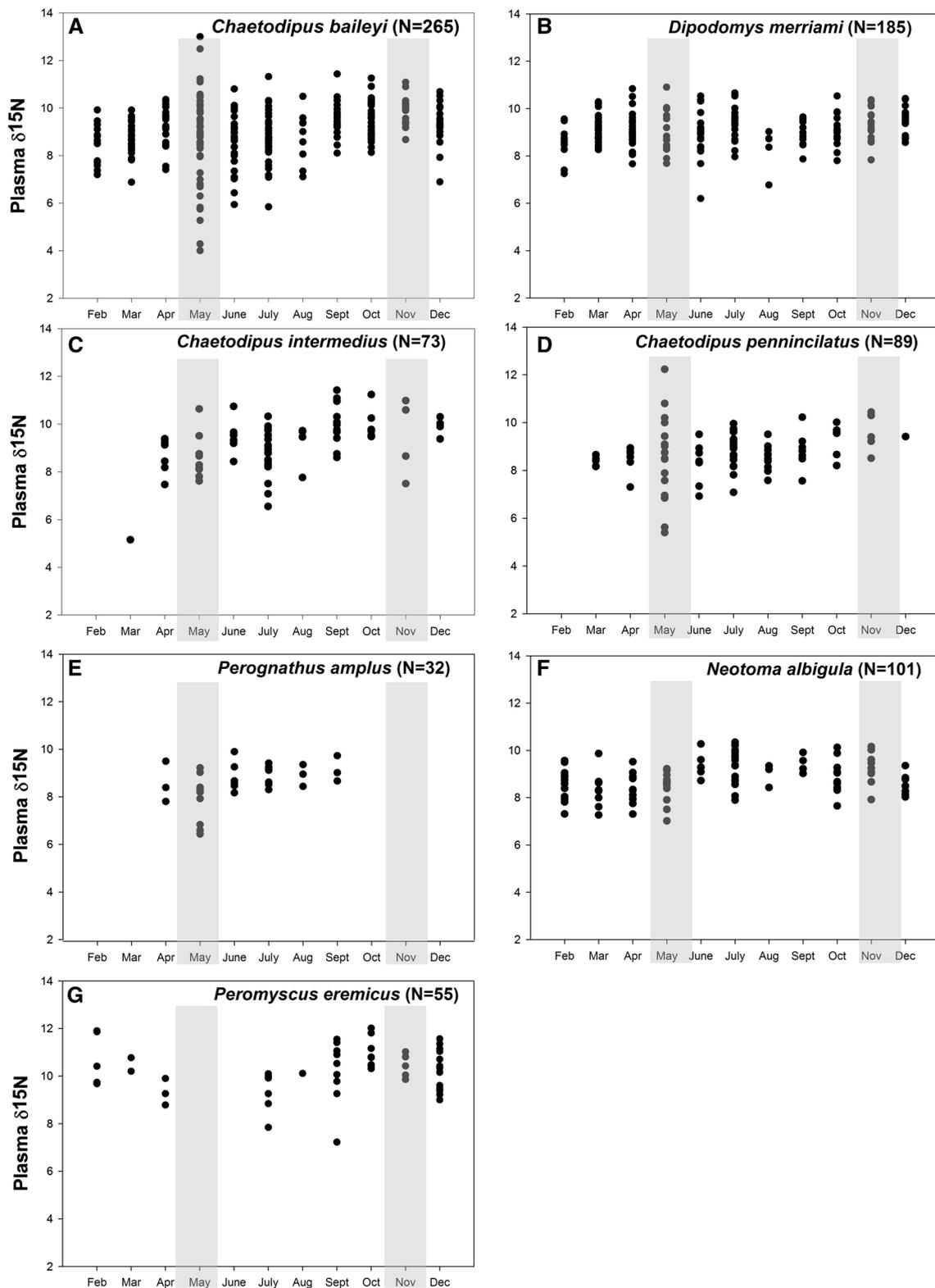
Relative trophic level was assessed from $\delta^{15}\text{N}$ measurements, and most species had mean $\delta^{15}\text{N}$ values ranging from 8.0 to 9.0 ‰ (Figs. 4, 5); some values were as high as 11 ‰, indicating greater use of arthropods or other animal materials. Plasma $\delta^{15}\text{N}$ values varied by month (ANOVA, $F_{10,812} = 6.296$, $p < 0.001$), and MANOVA revealed that species was a significant predictor of $\delta^{15}\text{N}$ ($F_{8,814} = 8.369$, $p < 0.001$), but neither site ($F_{1,812} = 0.149$, $p = 0.699$) nor sex ($F_{1,812} = 0.052$, $p = 0.820$) had a significant effect. Post-hoc Bonferroni tests revealed that both *Peromyscus eremicus* and *O. torridus* were significantly different from all other taxa ($p < 0.001$) but not from each other ($p = 0.146$). *Peromyscus eremicus* and *O. torridus* had mean (\pm SD) $\delta^{15}\text{N}$ values of 10.2 ‰ (± 0.5) and 11.5 ‰ (± 0.1), respectively, and values in both species ranged as high as 12 ‰, suggesting significant insectivory in some individuals (Figs. 4, 5).

Discussion

In this study, we used stable isotope analysis to carry out the first quantitative assessment of the importance of cacti as a nutrient resource to a desert rodent community. Our data show that the use of cactus resources varies greatly within the rodent community. Among the heteromyids, we predicted significant reliance on cactus seeds during the period when *C. gigantea* and *S. thurberi* were shedding fruit (H_1), but found that only two of five species showed a modest level of incorporation of cactus resources during this period. We predicted that there would be an extensive and potentially continuous use of cactus resources by cricetid rodents (H_2), but found that only *Neotoma albigula* and *Ammospermophilus harrisi* extensively used cactus resources throughout the year (Figs. 1, 2). We also hypothesized (H_3) that, because of their dry seed diet, heteromyid rodents would shift to consume more arthropods during the driest periods of the year, but found little evidence for this using $\delta^{15}\text{N}$ values as an indicator of trophic level. Below we discuss these results in detail and focus on: (1) the importance of cacti to individual consumers and seasonal variability associated with the shifting abundance of cactus seeds and pulp, (2) the relative trophic structure of the small mammal community as indicated by plasma $\delta^{15}\text{N}$ values, and (3) the potential role of cactus resources in the water economy of the small mammal community.

Fig. 3 $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ bivariate plots for each small mammal species (**a** *Dipodomys merriami*, **b** *Chaetodipus baileyi*, **c** *Chaetodipus intermedius*, **d** *Chaetodipus penicillatus*, **e** *Perognathus amplus*, **f** *Neotoma albigula*, **g** *Peromyscus eremicus*), showing the standard ellipse areas ($\%c^2$) for samples collected during the summer months (June–July, gray) and non-summer months (August–May, black). The mean ($\pm\text{SD}$) area ($\%c^2$) for summer (S) and non-summer (NS) ellipses are noted in each panel





Importance of cacti to the small mammal community

Cactus stems represent a dependable source of nutrients (and water) to some desert rodents. Hypothesis one (H_1)

predicted that the seasonal ripening of cactus fruit and the subsequent seed/pulp rain starting in early June would provide a large source of energy for primary consumers such as rodents. In our study area, where columnar cactus densities

◀ **Fig. 4** Plasma $\delta^{15}\text{N}$ values for rodents (**a** *Chaetodipus baileyi*, **b** *Dipodomys merriami*, **c** *Chaetodipus intermedius*, **d** *Chaetodipus penicillatus*, **e** *Perognathus amplus*, **f** *Neotoma albigula*, **g** *Peromyscus eremicus*) captured at our sites in Organ Pipe Cactus National Monument. *Black circles* indicate single-individual measurements during 2005 and 2006. Particularly dry periods at our field site occurred in May and November and lasted through February. These dry periods were coupled with extreme temperatures in May and November, making these particularly water-stressed times, so we hypothesized (H_3) that kangaroo rats and picket mice would shift to arthropods during the dry and hot period in the Sonoran (and thus enriched $\delta^{15}\text{N}$ values) in May through November (i.e., change starting and ending in the months *shaded gray*). Median plasma $\delta^{15}\text{N}$ values ranging from 8.0 to 9.0 ‰ represent primarily granivorous and herbivorous diets; median $\delta^{15}\text{N}$ values >9.5 ‰ represent insectivorous diets

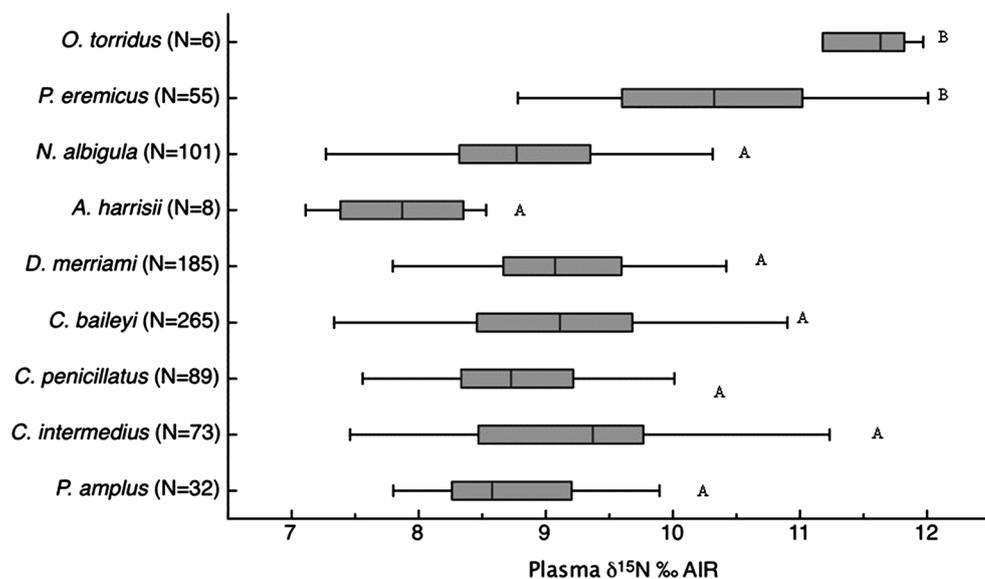
ranged from 20 to 60 plants/ha, cactus fruits represent a superabundant resource that is only partially exploited by the bird community (Wolf and Martínez del Río 2003). A simple estimate based on fruit production suggests that cacti could provide 100,000–200,000 kJ/ha if ~60 % of the fruit falls to the ground and the remaining 40 % is exploited by birds while fruits are still attached to the plant (Wolf and Martínez del Río 2003).

Despite this large pulse of nutrients, we found a large degree of variation in the relative importance of cacti to granivorous heteromyid rodents such as kangaroo rats and pocket mice (Figs. 1, 2, 3). Heteromyids showed both intra- and interspecific differences in cactus use. Standard ellipses (Fig. 3a–g) revealed clear seasonal differences in only three of five species. Consistent with our first hypothesis (H_1) that heteromyid rodents would utilize cacti during periods of fruit abundance, several species including *D. merriami*, *C. penicillatus*, and *P. amplus* largely ignored cactus resources most of the year, except during the peak

of seed rain in June–July; peak consumption of >10 % cactus resources was observed in only a few individuals during this time period (Fig. 2a, d, e). The two other granivores, *C. baileyi* and *C. intermedius*, consumed a considerable amount of cacti during June–July, with this resource representing 10–50 % of the incorporated carbon in many individuals (Figs. 2b, c, 3b, c). Several *C. baileyi* also showed extensive use (19.1–26.2 %) of cacti outside of the summer months (Figs. 2b, 3b), indicating that this species may rely on cactus seed caches throughout the year (Vander Wall 1990).

Given that columnar cacti shed several million seeds per hectare during the summer, it is surprising that cactus use is not more common among granivorous rodents. One possibility is that animal body size dictates the size of the seeds that rodents harvest (Price et al. 2000; Price and Mittler 2006). The seeds of saguaro and organ pipe cacti are small relative to those of most other C_3 plants. For example, saguaro seed masses average 1.3 mg (Steenberg and Lowe 1977), relative to a median seed mass of 67 mg in annuals and perennials (range 0.003–134 mg, $N = 26$ species) (Baker 1972; Wolf et al. 2002; Wolf, unpublished). At our site, only six of the 26 most abundant annual and perennial plant species have smaller seeds than saguaro. Despite their small size, cactus seeds are still readily used by some rodent species. The most intense user of cactus seeds among heteromyids, *C. baileyi*, is much larger (~25 g) than the other heteromyids we captured (*C. intermedius*, *C. penicillatus*, and *P. amplus*, ~11–16 g) that do not make extensive use of cacti; this pattern of use is in opposition to what might be expected based on the body size and seed size hypotheses (Price et al. 2000), and suggests that other factors such as nutritional demands (Chang and Zhang 2014) may be driving seed selection.

Fig. 5 Plasma $\delta^{15}\text{N}$ values of the rodent community; median (vertical line) and upper and lower quartiles (error bars) are shown. Median plasma $\delta^{15}\text{N}$ values ranging from 8.0 to 9.0 ‰ represent primarily granivorous and herbivorous diets; median $\delta^{15}\text{N}$ values >9.5 ‰ represent insectivorous diets. *Shared letters* indicate nonsignificant differences between groups at an α -level of 0.05 (ANOVA Bonferroni post hoc tests)



Seed toxicity may also determine, in part, which seeds are exploited by rodent species. Although the seeds of saguaro are not known to contain secondary compounds, seeds of at least two C_3 plant species at our site possess toxic secondary compounds. Both creosote (*Larrea tridentata*) and Jojoba (*Simmondsia chinensis*), which were equally abundant at the Uplands and Flats sites; possess seeds that contain high concentrations of secondary compounds (Sherbrooke 1976; Hyder et al. 2002). *Neotoma* can eat cacti stems as well as many other plants that contain toxic compounds, including creosote and jojoba (Dearing et al. 2000; Sorensen et al. 2004; Pichersky and Lewinsohn 2011). It is likely that *A. harrisii* has similar abilities given that it regularly consumes a diet of plant stems and leaves (Karasov 1982; Best et al. 1990), and *Chaetodipus baileyi* apparently eats jojoba seeds with no ill effects (Sherbrooke 1976; Hoffmeister 1986). In contrast, both *C. penicillatus* and *Dipodomys merriami* refuse to eat jojoba seeds in feeding experiments to the extent that they lose weight as a result of malnourishment (Sherbrooke 1976). Future work aimed at understanding resource utilization in the Sonoran Desert would benefit from considering the metabolic capacities of rodents in the context of plant-derived toxic compounds across a variety of plant species (e.g., Molokowu et al. 2011). Such research should evaluate both the digestive capacities of the various rodent species and quantify the concentration of toxins in seeds of plant species frequently eaten by desert consumers.

In contrast to heteromyids, the cricetid rodents captured at our study sites encompass several dietary guilds (herbivores, omnivores, and insectivores), and their utilization of cactus resources was expected to depend on these general foraging traits. Our second hypothesis (H_2) suggested that *P. eremicus* and *N. albigula* would extensively use the summer pulse of cactus fruit but also graze on cactus stems throughout the year to meet their water and energy requirements. Cricetids appear to have higher water requirements than heteromyid rodents (MacMillen and Hinds 1983) and use a variety of strategies to meet these water demands. For example, our observations and those of others (Vorhies and Taylor 1940; Spencer and Spencer 1941; Hoffmeister 1986) indicate that *N. albigula* grazes on cactus stems directly to obtain the water it needs (see Olsen 1976). Consistent with H_2 , the herbivorous *N. albigula* used cactus resources (primarily stems) to the greatest degree of all the rodent species we sampled (Figs. 1, 2f, 3f). The digestive physiology of *Neotoma* appears to allow it to negotiate the secondary compounds found in many cacti (Dearing et al. 2000; Sorensen et al. 2004; Pichersky and Lewinsohn 2011). In total, cactus resources accounted for an average 32 % of the annual incorporated carbon of *N. albigula* (Figs. 1, 2f, 3f), and in any given month, cactus use ranged from 0 to 80 % among individuals. Cactus resource use by

N. albigula peaked during June and July, with the standard ellipse for this period showing little overlap with the ellipse representing data from the rest of the year (Fig. 3f), which indicates a strong focus on both cactus stems and/or the fruit/seeds from columnar cacti during the summer. This is consistent with *N. albigula* experiencing increased water demands during this period. Alternatively, *N. albigula* may be exploiting the superabundant energy-rich pulp and seeds in addition to its use of stems for water. Others have also noted seasonal variation in the diet of *Neotoma*, associated with plant phenology as well as changing seasonal thermoregulatory demands (Dial 1988; Dearing et al. 2008). Grazing of stems during our study was restricted to *Opuntia* species, and we did not see evidence of grazing on large columnar cacti (*C. gigantea*). During extended periods of drought, however, *N. albigula* apparently shifts to grazing the stems of columnar species, producing staircase or candy-cane-like damage in otherwise healthy plants (Hayes et al. 2013). *N. albigula* may graze as much 30–40 % of the surface of a large *C. gigantea* (Online Resource 1 in the ESM), which results in a reduction in photosynthetic material, and has significant effects on cacti reproductive output but unknown effects on longevity (Hayes et al. 2013).

Although H_2 predicted that omnivorous cactus mice (*P. eremicus*) consistently use cactus stems for water, we noted that this species only used cacti during July, when this resource represented 20–60 % of its incorporated carbon (Fig. 2g). This seasonal shift was substantial, as shown by the nonoverlapping standard ellipses for summer versus other months (Fig. 3g). Interestingly, this shift in cactus use was accompanied by a ~ 1 ‰ decrease in mean plasma $\delta^{15}\text{N}$ values, suggesting that increased use of cacti may have replaced insects that were more frequently consumed during other periods of the year. Given the lack of cactus use by *P. eremicus* during other hot and dry periods of the year, it is likely that this species was exploiting abundant cactus fruit pulp and seeds for energy and not cactus stems for water. MacMillen's (1964) observations indicate that this species may estivate when nocturnal temperatures exceed 30 °C, which would result in lower water requirements during the summer; note that our trapping data generally support this observation (Fig. 2g), as we had lower capture rates of *P. eremicus* during the summer.

A third cricetid species, *O. torridus*, was captured occasionally ($N = 6$) and only at the Flats site during the course of our study. This primarily insectivorous species had the highest mean (\pm SD) $\delta^{15}\text{N}$ values (11.5 ± 0.5 ‰, Fig. 5) and has a large home range (O'Farrell 1978) relative to the other rodents we examined. The $\delta^{13}\text{C}$ value (-17.6 ‰) of the single individual sampled in July indicates that 37 % of its incorporated carbon was obtained from cacti (Table 3), which was accompanied by a decrease in $\delta^{15}\text{N}$ of ~ 1 ‰ (10.6 ‰) relative to the species mean, as would be

expected with a decrease in trophic level. While data from a single individual do not elucidate a pattern of resource use, this observation suggests that *O. torridus* directly exploits cactus resources when they are abundant. One might speculate that *O. torridus* are not using cacti directly during this period, but instead obtain cactus carbon indirectly from insects that eat cactus flowers or fruit. However, our stable isotope data for arthropods ($N = 305$, 10 orders, 18 families) indicate that cactus resources are exploited by only a few members of the insect community, including some small ants, a few beetles, and honeybees (Warne and Wolf, unpublished). Our limited data on insectivorous lizards also show no indirect use of cactus (Wolf and Martínez del Río 2003). The mean plasma $\delta^{13}\text{C}$ value (-21.3‰) for six species of lizards ($N = 22$) sampled between the last week in July and the first week in August indicated that the insects eaten by lizards did not consume cacti but rather C_3 plants (Wolf and Martínez del Río 2003). Similarly, throughout the rest of the year, our data suggest that *O. torridus* consumes primarily C_3 plants or insects that ingest C_3 plants (Fig. 1; Table 3). Despite the small sample size, our data are consistent with a previously reported pattern (Hoffmeister 1986) whereby this otherwise insectivorous species may shift to a lower trophic level during peak cactus production (July) and consume a greater proportion of cactus than during other periods of the year.

We also captured a limited number ($n = 8$) of diurnal *A. harrisii*. Although sample sizes were small, our data suggest that cactus resources were of significant importance to *A. harrisii* during the sampling period, and that they probably graze cactus stems similar to *N. albigula*. Captured in February–May and July, the mean $\delta^{13}\text{C}$ value for *A. harrisii* indicated that on average $\sim 52\%$ of their incorporated carbon was derived from cacti (Fig. 1; Table 3). Estimates of cactus carbon incorporation ranged from a low of 16% (April) to a high of 77% (July).

Trophic structure of the rodent community

Dietary studies of rodent communities in the American Southwest have noted significant differences in trophic level among species, which can range from strict herbivory to omnivory and even insectivory, and often vary on a seasonal basis. For granivorous species, such as heteromyid rodents, supplementing their diets with insects can greatly increase protein and water intake, providing the raw materials needed for reproduction or to balance water budgets during hot periods of increased water demand such as early summer (May–June), fall (September–November), or during winter drought. Seasonal shifts in diets can be difficult to detect, however, and often require invasive methods such as stomach content analysis. Measurements of $\delta^{15}\text{N}$ values in plant and animal tissues can provide insight into the

trophic structure of an animal community and how it varies temporally and spatially (Post 2002). Values of $\delta^{15}\text{N}$ predictably increase with trophic level such that values in consumer tissues are $\sim 3\text{--}5\text{‰}$ higher than those in tissues of their prey (Vanderklift and Ponsard 2003). During warmer periods defined by extreme water scarcity (early summer and fall), we hypothesized (H_3) that some species would show enriched plasma $\delta^{15}\text{N}$ values, indicating a shift to insects.

Plant $\delta^{15}\text{N}$ values (stems, leaves, fruit, seeds) collected from our study sites averaged $4.8 \pm 1.2\text{‰}$ SD (range $0\text{--}6.8\text{‰}$, Table 2); intra-annual variation in these values is not expected given that ^{15}N values are derived from soil nitrogen pools that are more persistent and have longer turnover rates than nitrogen in plant tissues (Evans and Ehleringer 1993; Amundson et al. 2003). Rodent plasma $\delta^{15}\text{N}$ values ranged from 4.0 to 13.0‰ (Figs. 4, 5), and most species in the community had mean $\delta^{15}\text{N}$ values that were $3\text{--}4\text{‰}$ above those of plants, indicating that they feed primarily on plant tissues (Fig. 4; Table 3). We did observe significant seasonal increases in plasma $\delta^{15}\text{N}$ in many rodent species, denoting the incorporation of insects into their diets. *Dipodomys merriami*, *C. intermedius*, *C. penicillatus*, *P. amplus*, *N. albigula*, and *A. harrisii* had the lowest mean $\delta^{15}\text{N}$ values, ranging from 8.0 to 9.1‰ , which suggest that these species were primarily herbivorous or granivorous. A few individuals of these species, however, had $\delta^{15}\text{N}$ values as high as 11‰ , indicating some use of insects (Figs. 4, 5). Indeed, previous work suggests that many granivorous species supplement their diets with insects (Reichman 1975, 1977; Thompson 1982; Tracy and Walsberg 2002; Hope and Parmenter 2007). Our data are consistent with those observations, and suggest that the peak period of arthropod use by heteromyid rodents as evidenced by increases in plasma $\delta^{15}\text{N}$ values was during September to November, with smaller peaks occurring during May and June. For example, five individuals of *C. intermedius* captured in the fall had plasma $\delta^{15}\text{N}$ values of $\geq 11\text{‰}$, suggesting a greater use of arthropods during this season, a pattern that supports H_3 .

Interestingly, the broadest range of $\delta^{15}\text{N}$ values was observed within a single species, *C. baileyi*, which had plasma $\delta^{15}\text{N}$ values that varied by nearly 10‰ among individuals and seasons ($4.0\text{--}13.0\text{‰}$): a range nearly twice that observed among the dominant primary producers in the system. Furthermore, the largest range in $\delta^{15}\text{N}$ among *C. baileyi* individuals was observed outside the summer months (Online Resource 2 in the ESM, Fig. 4). During this period, several *C. baileyi* had $\delta^{15}\text{N}$ values similar to the insectivorous *O. torridus* (12‰), while other *C. baileyi* had values $< 7\text{‰}$, indicative of a largely granivorous diet. This pattern suggests that some *C. baileyi* supplement their diet with insects and that, overall, this species is more of

a generalist consumer in comparison to the other granivorous heteromyids we sampled, especially in the spring and fall months when cactus fruits and seeds are not readily available.

The omnivorous *P. eremicus* had a mean $\delta^{15}\text{N}$ value of 10.2 ‰, and values often ranged above 11 ‰, indicating a shift to insectivory during much of the year. The lowest $\delta^{15}\text{N}$ values for *P. eremicus* occurred in July (mean $\delta^{15}\text{N} = 8.6$ ‰), when cactus use peaked at 39 % of incorporated carbon, suggesting an omnivorous diet during this month. Lastly, *O. torridus* had the highest mean $\delta^{15}\text{N}$ values (11.5 ‰), indicating that this species was primarily insectivorous. Like *P. eremicus*, the lowest $\delta^{15}\text{N}$ value for this species was obtained in July ($\delta^{15}\text{N} = 10.7$ ‰), when 38 % of the animal's incorporated carbon was derived from cactus resources. Again, this pattern suggests that both *P. eremicus* and *O. torridus* directly consume cactus resources during the summer, leading to a small but detectable drop in trophic level.

Cactus use and the water balance of rodents

The maintenance of water balance is a significant challenge for animals living in hot deserts, even though most of the rodent community is nocturnal (see Walsberg 2000; Tracy and Walsberg 2002). Balancing water budgets can be accomplished in a variety of ways, as exemplified by the members of this rodent community. At modest environmental temperatures (<25 °C), heteromyids may be able to survive on a carbohydrate-rich diet of dry seeds, which produces maximal metabolic water (Tracy and Walsberg 2002). In warmer environments, however, additional water is needed to balance their water budgets. Increased consumption of insects may not only be used to compensate for decreases in the abundance of other resources, but may also be used as a strategy for increasing water intake. Arthropods, which can be ~75 % water by mass (Bell 1990), were abundant at our sites from early March until the beginning of November (Wolf, personal observation) and represent a potentially significant source of water for animals that feed primarily on seeds that contain little free water. We observed increases in trophic level in heteromyid rodents in May and June (pre-monsoon) and from September to November (post-monsoon). May and June are hot and represent the driest months of the year, while the fall (September to November) can also be a period of high air temperatures and water scarcity. These observations suggest that the maintenance of water balance may be one of the primary forces driving heteromyids to consume arthropods more frequently during this period, which is supported by other studies (Reichman 1977; Thompson 1982; Tracy and Walsberg 2002). Maintaining water balance

may be less of a challenge for omnivores and insectivores such as *P. eremicus* and *O. torridus* because of their water-rich arthropod diets. However, even *P. eremicus* showed increases in plasma $\delta^{15}\text{N}$ values during the fall, which may yield increases in water intake via increased insectivory.

For herbivores, including *N. albigula* and *A. harrisii*, cactus stems may represent a critical resource during periods of heat and water stress. Stable isotope data indicate that both species appear to graze cactus stems extensively; because our data for *A. harrisii* are limited, we focus on *N. albigula*. Wood rats (*N. albigula*) made continuous use of cactus stems throughout the year, although use by individuals varied greatly. Cacti averaged 32 % of their incorporated carbon, and incorporation rates among individuals were as high as 80 % in a given month. Analysis of stomach contents ($n = 360$) in *N. albigula* by Vorhies and Taylor (1940) in southern Arizona found that cacti accounted for ~44 % of all food consumed, while insects comprised <1 % of total intake in a study that sampled 30 *N. albigula* each month for an entire year.

While cactus stems provide water, they also contain high concentrations of secondary compounds, which may limit their use by desert consumers (Gibson and Nobel 1986). *Neotoma albigula*, however, have the physiological machinery needed to effectively negotiate secondary compounds contained in cacti and other plants (Dearing et al. 2000; Sorensen et al. 2004) and the high water content of cactus stems (often >90 % by mass; Nobel 2002) dampens the intake of secondary compounds, even when cacti are frequently used as a resource. Vorhies and Taylor (1940) found that captive *N. albigula* would consume a combined mass of 50–70 g of fresh cactus stems and fruits of *Opuntia fulgida* daily, of which 45–63 g were water. Interestingly, none of the captives drank free water when it was offered. These observations are similar to those made in *N. albigula* in Death Valley, California, where several 20-L drinkers filled with deuterium-labeled water were hung in mesquite trees (the only dietary resource available) on paths frequented by *Neotoma*. Over a two-month period during the summer, none of the 50+ *Neotoma* sampled used the labeled drinker water (Wolf, unpublished data). Taken together, these observations suggest that when cacti are abundant, water stress is not a factor that limits the distribution and abundance of *Neotoma*, or likely those of other rodents (Hoffmeister 1986).

Conclusions

This is the first study to quantify the importance of cacti to a desert rodent community. We have shown that this seasonally abundant resource is important for only a few rodent species in the Sonoran Desert. This observation

is surprising given the large pulse of (food and water) resources released by cacti in the form of seeds and fruit pulp in addition to the large amount of water available in stems that persists on a day-to-day basis in this hot and arid landscape. We sought to test three hypotheses: (H_1) that granivorous rodents only seasonally use cacti as seed rain; (H_2) that herbivores use cacti stems year round as a source of water; (H_3) that granivores switch to insectivory to obtain water during hot months. We found that several species track the pulse of columnar cactus fruit resources (H_1) into the ecosystem during June and July, when these resources account for a small but detectable amount (~10–30 %) of their energy intake. For heteromyid species that use cacti, the cacti are likely to provide nutrients but not water, given that the known diets of these heteromyid species comprise dried seeds and that the periods during which they appear to use cacti match with the periods of cactus seed rain (Fig. 2). Consistent with H_3 , *Peromyscus* and *Onychomys* primarily fed on C_3 plant material and the insects that consume these plants, but both species shift to brief periods of cactus use during the hottest and driest months. In contrast, the larger cricetid *N. albigula* appears to be highly dependent on cactus stems as a year-round source of both water and energy (consistent with H_2). Because it grazes on the stems, this cricetid may have a significant impact on cactus abundance (Fig. 5). Our study extends traditional dietary studies of small mammals in deserts by quantifying the use of cacti, a potentially important source of both water and nutrients, and thus provides new insights into the interactions between consumers and this diverse group of New World plants.

Author contribution statement TJO and BOW conceived and performed experiments, SDN aided in the analysis, and TJO, SDN, and BOW wrote the manuscript.

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