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HOW IMPORTANT ARE COLUMNAR CACTI AS SOURCES OF WATER AND NUTRIENTS FOR DESERT CONSUMERS? A REVIEW

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Succulent CAM plants, such as columnar cacti, are important physiognomic elements of many arid lands. Although, these plants are often ecologically important because they provide abundant resources in the form of nectar and fruit, their contribution to the energy, nutrient and water budgets of consumers has not been quantified. We describe an isotopic approach that allows quantifying the ecological importance of CAM succulents. We first briefly review our work on the interaction between saguaros, an archetypical CAM succulent, and the desert doves that feed on its fruit. We then describe the potential importance of saguaro fruit as a function of its abundance, macronutrient composition, and seasonal availability. We argue that the resources provided by saguaros do much to satisfy the energy and water requirements of the birds that reside in hot subtropical deserts during the summer. We then describe the carbon isotope composition of saguaros and of the plant community in which they are imbedded and use two species of desert doves to illustrate how stable isotopes can reveal the importance of a single plant as a source of carbon and water for consumers. The second section of this review presents new data on the importance of saguaros for the entire community of birds that inhabit the Sonoran Desert during the summer. We show how the resources of saguaro reach across dietary guilds and account for a large proportion of the diet of many insectivorous species as well as that of granivorous and frugivorous species. We demonstrate that many of these species probably obtain significant water as well as nutrients from saguaro fruit. Finally, we point out the current limitations of using deuterium as a water tracer in animal systems.

Keywords: Carbon 13; Hydrogen 2; Natural variations; Nutrients; Plant-animal interactions; Review; Succulents; Water; Stable isotopes

INTRODUCTION

Succulent plants with CAM or C_4 photosynthesis are central physiognomic elements of many arid tropical and sub-tropical ecosystems [1]. Many plant communities in the arid zones of the New World are dominated by very large columnar cacti such as *Stenocereus*, *Carnegiea*, and *Pachycereus*, as well as smaller species such as prickley pears, *Opuntia spp.*, and agaves (Agavaceae) [2, 3] which use C_4 photosynthesis. In Africa, euphorbs (Euphorbiaceae) and

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aloes (Asphodelaceae) appear to have roles analogous to those of cactus and agaves in America [4]. Because many desert succulents produce abundant flower and fruit crops that are used by a variety of animals, they probably play an important role as foundation species [5], ecologically dominant species that provide significant amounts of resources to consumers (we use the term "foundation species" following Soulé and Noss [6]). In spite of the apparently obvious ecological importance of these plants, their functional importance as resource providers has not been quantified. How much do these plants contribute to the nutrient and water budgets of desert animals? Although this question could be asked for a variety of primary producers, CAM succulents may provide a particularly good system to answer it. This manuscript outlines an isotopic approach that aims to quantify the ecological role of a hypothetically important functional group of plants in desert ecosystems. We describe how stable isotope analyses have increased our understanding of the importance of a columnar cactus, the saguaro (*Carnegiea gigantea*), to the water economy and energetics of desert birds. Although we use the saguaro and the Sonoran Desert bird community as an exemplar, we believe that there is ample opportunity to use stable isotopes as tools to examine the interactions between succulent CAM plants and consumers in other ecosystems.

Our research relies on a simple but remarkable observation: the floral nectar, pollen and fruit pulp of saguaro have carbon and deuterium isotope values that differ from those of other available nutrient resources in the Sonoran Desert. These distinct isotope values provide markers that can be used to track the movement of materials from the saguaro into consumer tissues. Because some of our work on the isotopic ecology of saguaros has already been published, our description of methodological details will be cursory and general. Background materials can be found in Wolf [7], Wolf and Martinez del Rio [8] or in figure legends.

Our essay is structured in two broad components. The first, describes our previous results on the interaction between saguaros and desert doves. We describe in general, fairly qualitative terms, the potential importance of saguaro fruit as a resource. We depict its abundance, macronutrient composition, and seasonal availability. We also argue that the resources provided by saguaros do much to satisfy the energy and water requirements of the birds that reside in hot subtropical deserts during the summer. We then describe the carbon isotope composition of saguaros and of the plant community in which they are imbedded. We use two species of desert doves to illustrate how stable isotopes can reveal the importance of a single plant as a source of carbon and water for consumers. The second section of this review presents new data on the importance of saguaros for the entire community of birds that inhabit the Sonoran Desert during the summer.

THE ISOTOPIC ECOLOGY OF THE INTERACTION BETWEEN SAGUAROS AND DESERT DOVES

Saguaros as Resources for Nectar and Fruit-Eating Desert Animals

Cacti are prominent features of many arid and semi-arid ecosystems [3, 9]. They are widely distributed and abundant in the New World and because they can produce large crops of succulent fruit, they may play an important role in structuring food webs and ecosystems [3, 7, 8, 10–12]. Many cacti species are capable of storing immense amounts of water. Saguaros, for example, may be 90% water by mass and an individual can store 4000 or more liters of water [9, 13]. The succulent stems with their large capacity for water storage buffers many cactaceae from the notorious vagaries of precipitation in the desert. In the saguaro, it allows for the reliable year-to-year production of large numbers of flowers and fruit [14].

Mature saguaros produce, on average, 300 flowers each season with 50 to 60% of these setting fruit [15, 16]. Saguaros have apparently evolved to attract vertebrate pollinators and seed dispersers, and thus produce large quantities of nectar, pollen and succulent energy-rich fruits. Individual flowers produce about 1 ml of nectar in a single evening and 0.25 g of pollen that have energy contents of approximately 3 kJ and 6 kJ per flower, respectively. Saguaro fruits, like those of most other cacti, are notably large and moist and contain, on average, 19.4 ml water and 6.6 g (dry mass) of fruit pulp and seeds (with an energy content of approximately 90 kJ [7]). Saguaro seeds are abundant ($\approx$50% of the fruit's dry mass), relatively dry ($\approx$6.5% water content) and remarkably rich in proteins (16% dry mass, DM), lipids (30% DM) and carbohydrates (54%) [17, 18]. The fruit pulp in which these seeds are embedded, in contrast, is watery and the nutrients in it are primarily simple sugars. The difference in macronutrient composition between seeds and pulp has interesting consequences for consumers with different feeding modes. Granivorous species, that can grind the seeds, obtain proteins, lipids and carbohydrates. If they feed exclusively on seeds, they gain little water from saguaro. In contrast, the primarily insectivorous and carnivorous species that eat saguaro fruit when it is available obtain only water and sugars from the wet pulp and act as seed dispersers because they defecate intact seeds. Some species, such as White-winged Doves, assimilate both pulp and seeds and hence receive moisture, energy rich sugars, and superior nutrition from saguaro fruit [7]. Saguaros fruits represent a conspicuous, concentrated resource that can simultaneously meet both the water and energy requirements of many consumers.

Not only is saguaro fruit rich in water, energy, and nutrients, but it also is seasonally abundant in astounding quantities. During June, July and early August, a one-hectare stand of saguaros of moderate density (20 plants/ha), produces approximately 58,000 ml of water and 316,000 kJ of energy in fruit pulp [7]. At this density, these saguaros would produce adequate resources to satisfy the energy (field metabolic rate, FMR) and water requirements (water flux, WF) of 35 White-winged Doves (body mass ca. 150 g) for about 60 days (FMR in these doves is predicted to be about 130 kJ/day and WF about 28 ml/day, [19, 20]).

In addition to producing large amounts of resources, saguaros appear to time their flowering and fruiting phenology to a season of scarcity, when water and nutrients are most needed by consumers. In the Sonoran Desert, saguaros produce fruit during the driest and hottest period of the summer (June–July) just before the onset of monsoon rains. Shade air temperatures, which are a *minimum* index of the thermal stress, regularly exceed 50 °C for several hours and are commonly above 35 °C for over 12 hours each day. Exposure to sunlit areas and direct solar radiation produces an additional heat load that can be equivalent to approximately 20 times a bird's basal metabolism (typical basal metabolic rate of 50 Wm^{-2} versus 1000 Wm^{-2} for direct solar radiation) [21, 22] and may be physiologically equivalent to elevating air temperature by 8–12 °C [23, 24]. During the frequent periods where environmental temperatures exceed avian body temperatures (ca. 41–43 °C) [21] metabolic and exogenous heat loads must be dissipated solely through evaporation. As a consequence, avian evaporative water loss increases exponentially at higher environmental temperatures (Fig. 1). Most desert birds reduce activity and seek deeply shaded microsites during these periods. The result is a conflict between the demand to evaporate water for thermoregulation and the need to move to feed and drink maintain adequate hydration [25]. In spite of this observation, about 40 species of birds breed in the Sonoran Desert of Arizona during the summer [26]. Not only is the fruit of saguaro an

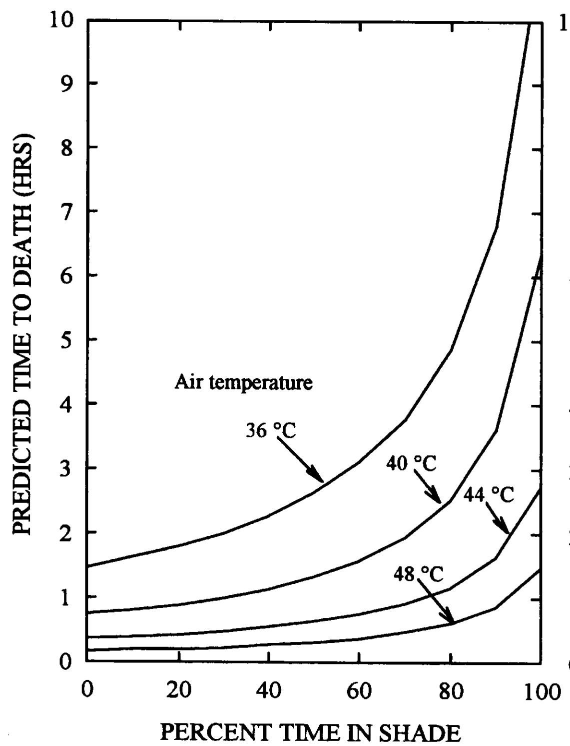

FIGURE 1 Predicted time to death for a small bird, the Verdin, (*Auriparus flaviceps*, ca. 6.5 g) that foregoes foraging activities during periods of high heat stress. Time to death is a function of microsite selection (% time in shade *vs.* % time in full sun) and air temperature (36, 40, 44, 48 °C). This model assumes that all foraging activity is suspended during periods of high stress. Indeed, desert birds, in general, reduce or suspend foraging activity drastically during periods of severe heat stress [47,48,49]. Each curve was produced by taking the Verdin's total evaporative water loss rate at the prevailing environmental temperature and then calculating the time required for the bird reach its limit of dehydration tolerance, *e.g.* lose 0.75 ml of body water. No excretory losses were assumed. Time to death is calculated assuming that perching in the sun raises environmental temperatures by 12 °C. Values for parameters are taken from [23,47,48,49].

attractive resource to a broad range of consumers including: insectivores, granivores and carnivores, it may be an essential one [10,27].

Saguaro has a Distinctive Carbon and Hydrogen Isotope Composition

As we noted above, the carbon isotope ratios of saguaro fruits are isotopically distinct from other resources available to avian consumers. The $\delta^{13}C$ of saguaro fruit averages $-13.1 \pm 0.2‰$ VPDB ($N = 29$) and exhibits little temporal variation [8]. The distinct isotopic value of saguaro is the result of its CAM (Crassulacean Acid Metabolism) photosynthetic pathway. Although other cactus species inhabit the study area, there are differences in phenology and consumer use; Englemann's prickly pear, *Opuntia engelmannii*, for example, is the second most abundant (in biomass) animal dispersed cactus after saguaro and produces fruits that mature at the end of the summer. These fruits appear to be consumed mostly by mammals rather than by birds (Wolf, per obs.) [2]. There are also very limited numbers of C_4 plants in this region that are used by consumers. Most represent a very small portion of the total ecosystem biomass and are not used by avian consumers. In an analysis of the contents of approximately 160 White-winged and Mourning Doves crops, for example, the seeds from only one C_4 plant were found (*Kallastroemia grandiflora*) and these represented less than 0.5% of the total seeds by mass [7, 8]. Thus, saguaros are the only CAM resource of significant biomass available to consumers for several months. As saguaro fruits ripen, a pulse of nutrients with this CAM signature enters the foodweb and is superimposed on a resource base composed of annual and perennial plants that use C_3 photosynthesis and hence have isotopic compositions that contrast with those of saguaro. Seed samples obtained from the most common species of C_3 plants on the study area (*Amsinckia*, *Acacia*, *Calliandra*, *Cercidium*, *Eschscholtzia*, *Fouquieria*, *Jatropha*, *Lysium* and *Prosopis*) had an average $\delta^{13}C$ of -24.9 ± 0.2 SE ‰ VPDB ($N = 12$).

The water in saguaro fruit pulp also has distinctive hydrogen isotopic composition relative to that of available surface water. In 1998, the δD of saguaro fruit during averaged 48.4 ± 1.6‰ VSMOW ($n = 82$) and was very constant in time. In contrast, water in catchments was isotopically lighter (from -37.3 to -23.5‰ VSMOW, from mid-May to 30 June) and its deuterium content was more variable. The temporal variability in the isotopic composition of catchment water was a result of monsoon rains, which starting in July periodically refilled catchments with water that was depleted in deuterium compared to catchment water. Although available surface water showed some isotopic variation over time, the water provided by saguaro fruit was isotopically distinct from the water in catchments. In a subsequent section we will describe the challenges posed by the use of deuterium composition to track water use. Here it is sufficient to state that the water in saguaro fruit is sufficiently enriched in deuterium to allow assessing, at least qualitatively, the importance of saguaro fruit as source of water.

Use of Saguaro by Desert-Nesting Doves

Differences in carbon isotope values between the saguaro and other plant resources have enabled us to examine the importance of the saguaro to the nutrient and water balance of two species of desert-nesting doves. In these studies [7, 8], we used both stable isotope (liver tissue) and crop content analyses to assess the importance of saguaro fruit as a source of nutrients and water for White-winged (*Zenaida asiatica*) and Mourning Doves (*Zenaida macroura*) and to validate the use of stable isotopes as resource tracers. Using stable isotopes we found a significant difference in saguaro use between these two species; in White-winged Doves saguaro fruit comprised greater than 60% of their diet between June and mid September. In addition, the $\delta^{13}C$ and δD of liver tissue and body water were linearly and positively correlated, indicating that saguaro fruit was an important source of both carbon and water. In contrast, Mourning Doves only gained nutrients (about 35% of total carbon) from saguaro during a period of about three weeks in July. In Mourning Doves there was no correlation between $\delta^{13}C$ and δD with increased saguaro use. The δD of body water remained unchanged as the carbon in liver tissue enriched with increased saguaro use. Thus, Mourning Doves relied on saguaro fruit as a source of nutrients, but not of water. These observations agree with the general observation that White-winged Doves foraged from the tops of saguaros where they had access to ripe fruit containing both water and nutrients whereas the Mourning Doves foraged only from the ground where the dried saguaro fruit had fallen. Stable isotopes revealed that a single food can provide congeneric sympatric species with a different suite of resources as a consequence of the species' foraging mode. Thus, the resources obtained by a consumer are the result of not only resource characteristics, but also of the interaction of the resource traits with the consumer's behavioral and physiological traits. Stable isotope methods provide a unique opportunity to isolate and characterize many of these interactions.

SAGUAROS AS NUTRIENT SOURCES FOR A DESERT BIRD COMMUNITY

Measuring How Important Saguaro Really is? Faithfullness and the Time Scale of Isotopic Incorporation

Our research on saguaro use by desert doves suggests that saguaro fruit is a crucial resource for these animals. Extending these observations and determining the importance of saguaro for the community of Sonoran Desert birds is, however, a more complex task. It requires making a temporal sequence of measurements of the isotopic composition of the tissues of as many species as possible. It also requires making some simplifying assumptions. This section deals with these assumptions.

Determining the proportion of an animal's diet that is represented by two isotopic sources is commonly performed using a mixing model [28, 29]. Although there are a variety of mixing models with varying degrees of detail and sophistication [30], we have used the simplest one:

$$\delta_{\text{tissue}} = p(\delta_1 + \Delta) + (1 - p)(\delta_2 + \Delta) \qquad (1)$$

where p is the fraction of the diet that is incorporated into the focal tissue, δ_1 and δ_2 is the isotopic composition of the two sources and Δ is isotopic discrimination factor. Using this model requires considering both the endpoint values of the two sources and the diet to tissue isotopic discrimination factor. For carbon sources, we have used the isotopic composition of saguaro ($\delta^{13}C \approx -13‰$) and C_3 plants ($\delta^{13}C \approx -25‰$) as endpoints.

The faithfulness of incorporation of a resource into an animal's tissues is rarely perfect. There often is some difference in the isotope value between the consumer's diet and its tissues [31–36]. This difference between the isotopic composition of resources and a consumer's tissues is the "discrimination factor" ($\Delta = \delta_{\text{tissues}} - \delta_{\text{diet}}$) [32, 37]. In our previous work, we used the discrimination factor for liver tissue to diet given by Hobson and Clark [32]. For the whole avian community, we are measuring the $\delta^{13}C$ of blood plasma thus we had to establish a community wide diet to plasma discrimination factor. Data from earlier work on Mourning Doves [7] and data depicted in Figure 2 provided a tentative estimate of the diet to plasma carbon discrimination factor that can be applied at the community level. Laboratory experiments are needed to assess the reliability of this estimate.

Figure 2 illustrates a temporally stable C_3 resource signal in bird plasma during the periods surrounding saguaro fruit ripening. The mean $\delta^{13}C$ of plasma for avian consumers before (May–early June, average $-21.4 \pm 0.26‰$, $N = 33$) and after (August, average $-21.8 \pm 0.22‰$) the period of saguaro availability are not significantly different (average $\delta^{13}C$ $-21.6 \pm 0.2‰$, $N = 65$, t-test, $T = 1.12$, $P = 0.26$, $N = 65$). These values are also very close to the values observed in Mourning Dove tissues during the same periods in the previous year (1998) [7], indicating that this base resource $\delta^{13}C$ is apparently stable from year to year. Finally, the signal appears to be stable across different classes of vertebrates as suggested by plasma samples obtained from Clark's spiny lizards (*Sceloporus clarkii*) during the peak of saguaro fruit production in June of 2001 ($-20.9 \pm 0.2‰$ VPDB, $N = 7$; B. O. Wolf and C. J. Wolf unpublished data). Note that more positive average $\delta^{13}C$ presented in Figure 2 for early May includes Neotropical migrants that are passing through the desert and potentially fed from C_4 or CAM sources farther south. Thus, the apparent diet to plasma discrimination factor is approximately equal to the difference between $\delta^{13}C_{\text{plasma}} - \delta^{13}C_{\text{plants}} = [(-21.6‰) - (-24.9‰)] = +3.3‰$. Combined with the mixing model, these fractionation data provide a means of estimating the proportion of a consumer's diet that is derived from saguaro.

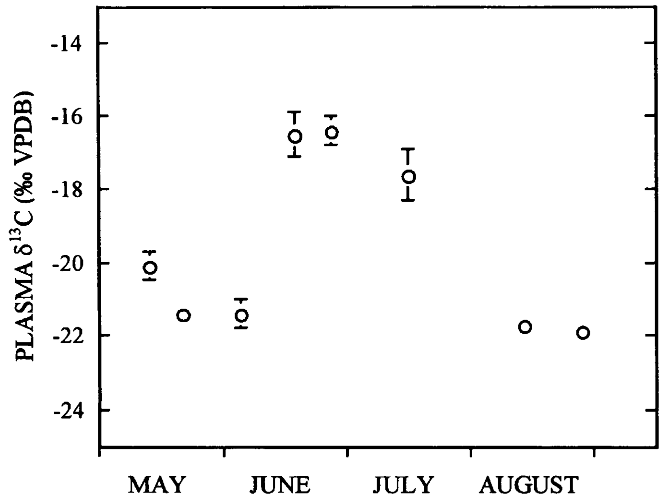

FIGURE 2 The $\delta^{13}C$ of the blood plasma of the bird community changes as saguaro fruit becomes available. Data were collected from May until August of 2001. Each point is a mean ± SE ($N = 15$–30 individuals, see Tab. I for specifics). Birds were sampled weekly by mist netting. A small blood sample (50–150 μl) was taken from the wing vein of each individual. Blood was centrifuged and the isotopic composition of plasma was measured. Carbon isotope measurements were obtained by introducing approximately 0.2 mg of dry plasma wrapped in a pre-cleaned tin capsule into a Carlo Erba elemental analyzer interfaced with a Finnigan Delta Plus XL continuous flow mass spectrometer. Precision of these analyses was ±0.2‰. Birds were netted in a desert wash in the Sand Tank Mountains (Maricopa County, AZ). The vegetative community is classified as part of the Sonoran Desert upland subdivision. Saguaro densities on the capture sites ranged from 30 to 60 plants per hectare.

Phillips and Gregg [38] have recently described how endpoint source variation can influence the confidence with which dietary proportions can be estimated using a mixing equation (*e.g.* Eq. (1)). They conducted a series of simulations to quantify how source variances, differences in endpoint distances and sample (consumer) variances and sample sizes affect estimates of proportion derived from the mixing equations. One of their conclusions was that when source variances were smaller than the variances in the sampled population (*e.g.* consumer tissue), the source variances have little overall affect on the confidence with which the proportions are estimated. These observations support our use of community baseline $\delta^{13}C$ values for use in estimating a discrimination factor. The $\delta^{13}C$ values in Figure 2 collected from consumer tissues, in May and August, have smaller variances than those measured in consumers in June when the saguaro is producing fruit. This is necessarily the case, because in May, only C_3 sources are available and these variances are small compared to the variance that is introduced into the system when birds are feeding from both CAM (saguaro) and C_3 resources.

In addition to accounting for potential differences in isotopic composition between a resource and a consumer, isotopic studies of resource transfer must account for another important confounding effect. Different tissues turnover their carbon pools at different rates. Blood plasma proteins and liver show much higher turnover rates than muscle and red blood cells, and these have higher rates than bone collagen [33, 39]. The temporal window of isotopic incorporation depends on the carbon turnover of a tissue. The isotopic composition of tissues with high turnover (plasma proteins and liver) reflects the temporal average of the isotopic composition of the carbon incorporated recently. In contrast, tissues with very low carbon turnover (*e.g.* bone collagen) may reflect the average composition of the carbon incorporated over an individual's lifetime. Because we were interested in measuring the rate at which saguaro carbon was transferred into consumers, we chose to measure the isotopic composition of blood plasma proteins. Hobson and Clark [33] have shown that the carbon half-life for plasma is short (about 3 days in Japanese Quail, *Coturnix japonica*). Thus, assuming that the turnover of carbon in plasma is similar among bird species, each of our samples averages the isotopic composition of an individual's diet over about a week-long period. Again, this estimate is preliminary and contingent on laboratory measurements of carbon turnover in the plasma of the species that consume saguaro fruit.

Saguaro Use by the Avian Community: A Preliminary Report

Seeing very different patterns of saguaro use and dependence in White-winged and Mourning Dove suggests that there may be large differences in the utilization and importance of saguaro fruit within the bird community in general. Taken as a whole, the community shows a striking pattern; the $\delta^{13}C$ of plasma in the bird community during the summer shows a distinct "swell" that corresponds with the input of saguaro fruit into the ecosystem (Fig. 2). As we noted earlier, before the production of saguaro fruit, the community at large had an average $\delta^{13}C$ value of about −21.6‰ VPDB. The community-wide plasma isotopic composition increased rapidly in mid-June to a relatively high value (−16.4‰). Using the mixing model presented above (Eq. (1)) and a diet to plasma discrimination factor of +3.3‰ indicates that about 43% of the entire avian community's carbon was derived from saguaro fruit during this period. Using plasma proteins, as our probe of the importance of saguaro, the saguaro's influence on the nutritional ecology of the bird community appeared to last about six weeks. We intentionally excluded doves from Figure 2 because we wanted to present data that represented a localized resource pulse on a few hectare scale (See Tab. I for individual species sampled and isotopic values.). Doves forage over spatial scales of thousands or tens of thousands of hectares, thus, analyzing dove samples would have integrated saguaro availability and use over a regional scale. Recall that Wolf and Martinez del Rio [8] found that White-winged Doves exploit the saguaro resource from early June until the middle of September, a period of about 12 weeks. Thus, we might make the generalized prediction that, because of spatial and temporal variation in fruit ripening and availability, consumers with larger home ranges will have access to the fruit resource for longer periods and consequently utilize saguaro fruit over a longer period [8, 14, 40]. These examples show how stable isotopes can potentially detect resource use that is a function of body size and/or individual scale of movement.

Because we are looking at the whole bird community, we need to consider whether the insectivorous species that show a saguaro signal when fruit are abundant are actually eating saguaro fruit. These species, such as Ash-throated and Brown-crested Flycatchers, could be consuming insects that eat saguaro fruit. Our observational data suggest that this is not the case; saguaro fruit is not apparently used extensively by insects. Birds apparently obtain the carbon signal directly from the plant. These observations are supported by the brilliant red, seed laden, excreta that these species leave behind when they are handled. Some species of ants may pick up the seeds once the fruit falls to the ground, but we rarely see any insects on the fruit while it is attached to the plant. We do not discount the possibility of this indirect carbon transfer, but we currently lack any evidence and no systematic studies have been carried out. The lizard measurements presented above also support this view; spiny lizards are insectivores and even during the peak period of saguaro fruit production their plasma carbon isotope values remain at the C_3 baseline values that are seen in birds before and after the period of fruit ripening. It is more likely that there may be some indirect transfer of carbon into the bird community during the period of flower production. During this period, saguaro flowers are heavily visited by insects and birds, and the nutrients contained in the saguaro's pollen and nectar could be transferred to the bird community through insect consumption. This area remains unexplored.

TABLE I Plasma Carbon Isotope Ratios (‰ VPDB) of the Bird Community by Species and Date Sampled.

SPECIES/DATE	*5/12/99*	*5/20/99*	*6/3/99*	*6/13/99*	*6/16/99*	*6/30/99*	*7/14/99*	*8/11/99*
Amphispiza bilineata		−21.1		−15	−17.1	−16.4 ± 0.6 (2)	−20.3	−22.5 ± 0.2 (2)
Callipepla gambelii		−22.2 ± 0.2 (2)		−21	−21.4	−17.2 ± 0.1 (2)		
Campylorhynchus brunneicapillus	−19.5					−20.6	−20.47	−21.6 ± 0.1 (2)
Cardinalis cardinalis							−20.9	
Cardinalis sinuatus	−21.2							
Carduelis psaltria					−19.2			
Carpodacus mexicanus	−21.9 ± 0.6 (3)	−20.1 ± 0.9 (4)	−19.7 ± 0.4 (2)	−14 ± 0.3 (5)		−14.8 ± 0.1 (2)		−20.5
Colaptes auratus							−15.7	
Dendroica petechia								
Dendroica townsendi		−21.3						
Empidonax difficilis	−19.39							
Icterus cucullatus								
Icterus parisorum							−17.4	
Melanerpes uropygialis	−16.1 ± 0.5 (2)			−14 ± 1 (2)				
Melospiza lincolnii		−22.5						
Mimus polyglottos						−17.4		
Molothrus ater				−17.1				
Myiarchus cinerascens		−21.8 ± 0.8 (2)	−21.5 ± 0.6 (3)	−16.4 ± 0.2 (2)		−17.5 ± 0.6 (5)	−16.5 ± 1.4 (5)	−22.2
Myiarchus tyrannulus				−16.8 ± 3.2 (2)	−17.2 ± 0.5 (3)	−17.5 ± 0.6 (5)		−22.3
Oporornis tolmiei						−15 ± 1 (3)		
Passerina amoena			−21.4			−15.9		
Passerina versicolor						−14.8	−19.7	
Pheucticus melanocephalus	−20.3 ± 0.6 (4)		−22.5 ± 0.8 (5)					
Pipilo chlorurus	−21.4							
Pipilo fuscus	−20.1 ± 0.2 (2)		−20.7				−16.8 ± 0.4 (2)	
Piranga ludoviciana		−22.0 ± 0.5 (3)			−21.1			
Toxostoma curvirostre	−18.72		−18.9 ± 0.2 (2)			−13.6		−20.8
Vireo gilvus		−21.4						
Wilsonia pusilla	−21	−22.2						
Zenaida asiatica	−17.6		−19.9 ± 1.0 (2)	−14.3 ± 0.6 (2)	−16.4 ± 0.9 (6)	−15.1	−15.9	
Zenaida macroura	−23.4	−24.7 ± 0.2 (3)	−24.2 ± 0.3 (4)	−23.5	−25.0 ± 0.2 (2)	−20.2 ± 2 (3)	−24.0 ± 3.5 (2)	−21.7 ± 0.4 (2)

Note: These data are summarized in Figure 2. Data presented are means ± SE and (*N*) where more than one individual was captured on a single day. Values for *Zenaida macroura* and *Z. asiatica* are included for completeness, but were not used in Figure 2.

We can also look at the importance of saguaro to individual species within the community. Figure 3 provides snapshot of the relative importance of the saguaro to a group of consumers over a period of about ten days. These data were collected during the peak of saguaro fruit availability, during the middle of June. We might reasonably expect that saguaro would be a primary component of the diets of granivorous and frugivorous species. Indeed, saguaro seems to account for 60 to 70% of the diet of House Finches, Varied Buntings, Brown Headed Cowbirds and Lesser Goldfinches, 50 to 60% of Canyon Towhees and Mourning Doves, and 40 to 50% of the diets of six other species from a variety of dietary guilds. Among this latter group, is four primarily insectivorous species that include: Brown-crested Flycatcher (50%), Cactus Wren, (47%), Verdin (48%) and Curve-billed Thrasher (46%). Strikingly, 7 of the 16 species where saguaro comprises more than 25% of the diet are considered primarily insectivorous. The rate at which species continue to exploit saguaro varies from species to species and in mid-July, when saguaro fruit abundance has declined markedly (ripe fruits occur on less than 5% of the plants versus 40% during the June sampling period), some species such as Curve-billed Thrashers ($47 \pm 4\%$ SE, $N = 7$), House Finches ($59 \pm 4\%$ SE, $N = 7$) and Gila Woodpeckers ($65 \pm 2\%$ SE, $N = 2$) continue to favor saguaro whereas others such as Brown-crested Flycatchers ($17 \pm 4\%$ SE, $N = 4$), and Canyon Towhees ($21 \pm 4\%$ SE, $N = 3$) shift to other food resources. Unfortunately, our sample sizes are still too small to assess with confidence the degree of reliance of different species on saguaro as a function of saguaro availability.

Using Deuterium as a Label for Resource Tracking

So far, our analysis of saguaro use by a bird community has revealed that this plant is an important carbon (*i.e.* energy and organic nutrients) source. Can we use the deuterium composition of

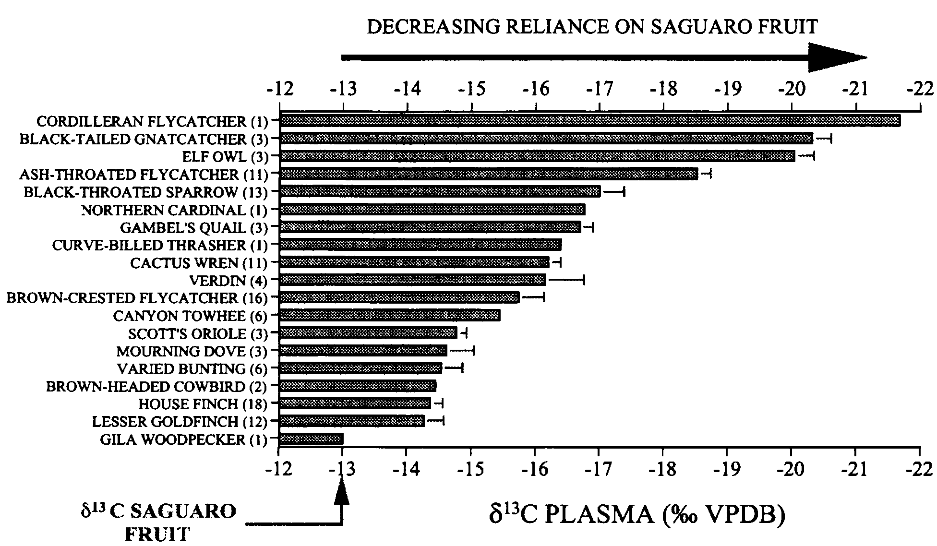

FIGURE 3 Interspecific variation in the $\delta^{13}C$ of plasma collected from members of the bird community nearing the peak of saguaro fruit maturation (6/18/01–6/22/01). Using the mixing model (Eq. 1 in text) and assuming a diet to plasma discrimination factor of 3.3‰ yields fractional utilization rates that range from 0% (Cordilleran Flycatcher) to 75% (Gila Woodpecker). A 1‰ increase in the $\delta^{13}C$ of tissues equals about an 8% increase in saguaro carbon incorporation. $\delta^{13}C$ endpoints used in the mixing model for saguaro and C_3 resources were −13‰ and −24.9‰ VPDB, respectively. Each bar represents a mean ± SE (not visible). Sample sizes (N) are shown in parentheses (Wolf and Martinez del Rio, unpublished data).

plasma water to assess the importance of saguaro as a water source for the avian community? The δD of saguaro fruit water is enriched by 75 to 100‰ over other water resources in the environment. The existence of this signal should potentially allow estimation of the fractional importance of the water obtained from saguaro to the water balance of individual members of the bird community. To our knowledge, this has not been attempted in other study systems. Working with White-winged Doves, we have found that the body water pool of birds using saguaro fruit becomes enriched in deuterium (Fig. 4) and that there is a strong correlation between $\delta^{13}C$ of liver tissue and δD body water that indicates the doves are simultaneously incorporating water and nutrients from saguaro fruit [8]. However, the dove's body water appears to show a large source to body water discrimination factor. The δD of the dove's body water is enriched well above that of the saguaro resource signal. We have more recently found this same phenomenon in other avian species consuming saguaro fruit (Fig. 5).

A possible explanation for this observation is that birds lose a significant amount of light (*i.e.* D depleted) water and hence their body water is enriched in D. Because water in urine and feces appears to have the same isotopic composition as body water, the most likely venue for this fractionated water loss is evaporation [41,42]. Indeed, evaporative losses can be extremely high in desert birds [23], and thus the deuterium enrichment of body water in desert birds is perhaps not surprising. Although it is tempting to apply a simple mixing model to estimate the contribution of saguaro to the water balance of birds, this may be difficult. We are just beginning to understand the determinants of the hydrogen isotopic composition of body water. Only a small number of researchers have dealt with this subject in animals and a significant amount of the published work is focused on the potential problem that this large evaporative enrichment in deuterium poses for doubly labeled water studies [42–44, reviewed by Speakman 45].

Using deuterium to estimate accurately the importance of saguaro as a water source for birds may prove to be difficult. This does not mean that measuring the deuterium content in body water will be uninformative. For animals feeding on saguaro, water and nutrient

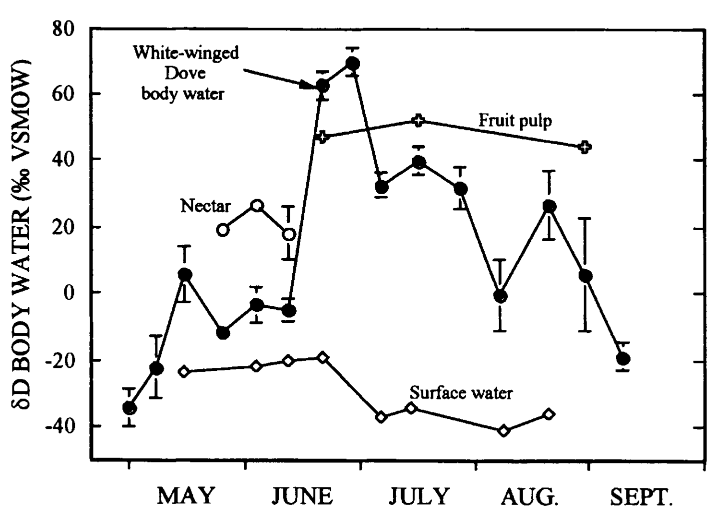

FIGURE 4 Temporal changes in the hydrogen isotope composition of the body water of White-winged Doves follow the fruiting phenology of saguaro. Note that during the peak of saguaro fruit production, the bird's body water becomes more enriched in D than the water in saguaro fruit. Also shown are the hydrogen isotope compositions of water Arizona Game and Fish Water catchments (labeled *surface* water) and of the water in saguaro floral nectar and fruit pulp [8].

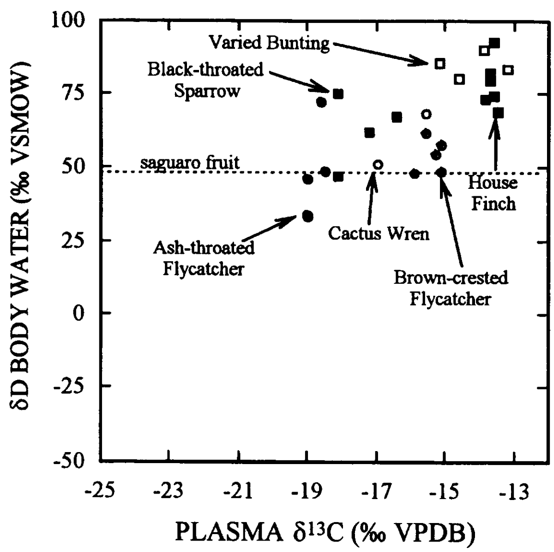

FIGURE 5 Hydrogen and carbon composition of body water and plasma for select members of a bird community during the height of saguaro fruit production (06/18/01–06/22/01). Note that both the granivorous species (boxes) and insectivorous species (circles) co-enrich in both isotopes when consuming saguaro fruit. This indicates that both species are foraging from the tops of saguaros (not the ground) and that both groups are incorporating carbon. Also note the body water pool of most species is enriched deuterium above that of the saguaro (Wolf, unpublished data). δD measurements were obtained by micro-distilling water from plasma [50] and then repeatedly injecting 1 microliter of this water into a Finnigan TC/EA pyrolysis device interfaced with a Finnigan Delta Plus XL continuous flow isotope ratio mass spectrometer. Three to five injections were made for each sample and the precision of this analysis using lab waters was ± 1.5‰ SD VSMOW.

movement tend to be tightly linked for many consumer species, [8, and Fig. 4]. Recall that in White-winged Doves $\delta^{13}C$ and δD were tightly correlated indicating that birds used saguaro as both a water and a carbon source. In Mourning Doves, in contrast, $\delta^{13}C$ and δD were uncorrelated indicating that birds used saguaro as a nutrient source exclusively. At the very least, the presence or absence of correlations between $\delta^{13}C$ and δD can be used to diagnose whether birds feed primarily on the relatively dry, but nutrient rich, seeds or if they ingest the moist pulp as well [7]. For pulp feeders, which can be diagnosed by a positive $\delta^{13}C$ and δD correlation, we can use carbon isotopic data from plasma proteins to estimate the amount of water that birds obtain from feeding on saguaro. Birds appear to focus on fresh fruits that are unopened or newly opened (B. O. Wolf, unpublished). In these fruits, the dry matter (*i.e.* carbon) to water ratio is relatively constant (three grams of water for every gram of dry pulp). This observation provides an independent way to estimate water flux from the plant into consumers.

CONCLUSIONS

We hope that our candid overview of the isotopic ecology of this saguaro/consumer interaction has identified what we know and what we do not know about this system. It is readily apparent from our initial isotopic measurements that the saguaro is a resource of unparalleled importance to the Sonoran Desert bird community during the summer. Concurrent measurements of $\delta^{13}C$ and δD have revealed that saguaro provides nutrients to many species, and nutrients and water to a subset of these species. We believe that the temporal variation of

$\delta^{13}C$ in plasma provides accurate estimates of the importance of saguaro as a nutrient and energy source. Although δD provides a qualitative indicator of saguaro as a water source, it provides only a qualitative assessment of its importance to the bird community's water budget. Using δD is contingent on a better understanding the factors that lead to the large dietary water to body water differences that we often observe.

As ecological physiologists, we would like to measure the contribution of the saguaro to the water and energy budgets of individual birds. As ecologists, we would like to know how the saguaro's importance varies across foraging guilds and what are the factors (body size, foraging mode, digestive physiology) are that influence the saguaros importance to individual species. At a broader scale, we would like to know if the consistent year to year production of abundant water and nutrients in saguaro fruits provide a stabilizing influence on community structure by dampening variation in resource availability. Although we have focused on saguaros, we point out that the approaches that we have described here can be used in a variety of communities in which CAM plants are found. In the Karoo of Southern Africa succulent euphorbs and aloes make up 32% of the flora and up to 70% of the species abundance and cover [46]. In the Tehuacán valley of Mexico the density of columnar cacti reaches an astounding 1200–1800 plants per hectare [3]. What is the ecological importance of these plants? Clearly the approach that we have described can be used in these ecosystems. Although most of the questions that we have posed in this section remain unanswered, we hope to have demonstrated that stable isotope methods are key tools in ecological research that aims to estimate qualitatively the ecological importance of CAM plants to consumers in desert ecosystems.

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