STABLE ISOTOPES REVEAL THAT SAGUARO FRUIT PROVIDES DIFFERENT RESOURCES TO TWO DESERT DOVE SPECIES

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Abstract. During the Sonoran Desert summer, saguaro cacti produce an abundant fruit crop whose nutrients and water have distinctive stable isotope compositions. Carbon stable isotope analyses indicated that, at the peak of saguaro fruit production, saguaro fruit represented >90% of White-winged Dove and ~50% of Mourning Dove carbon incorporation. Over the entire summer, saguaro fruit comprised 50% and 14% of the diet of White-winged and Mourning Doves, respectively. In White-winged Doves, δ^{13}C of their liver tissue and δD (deuterium) of their body water were linearly correlated, indicating that saguaro fruit was an important source of both nutrients and water. In Mourning Doves, in contrast, δ^{13}C and δD were not correlated. Mourning Doves acquired nutrients but not water from saguaro fruit. Stable isotopes revealed that a common food plant sometimes provides a very different suite of resources to the different species that consume it.

Key words: Carnegiea gigantea; differential resource use; Mourning Dove; resource utilization; saguaro cactus; Sonoran Desert, Arizona (USA); stable isotope ratios; White-winged Dove; Zenaida asiatica; Zenaida macroura.

INTRODUCTION

The saguaro cactus (*Carnegeia gigantea*) is a massive, long-lived, columnar cactus that occurs throughout much of Arizona (United States) and Western Sonora, Mexico (Turner et al. 1995). Saguaro fruit are seasonally abundant and their pulp is rich in nutrients and water (Haughey 1986). On average, the pulp of a single fruit weighs 26.0 ± 14.8 g (mean ± 1 SD, N = 79), of which 6.6 ± 3.6 g is dry material and 19.4 g is water. Ripening of fruit typically occurs from June through August (Haughey 1986, Fleming et al. 1996, Wolf and Martínez del Rio 2000) during the driest and hottest periods of the summer (AZMET 1999). Long periods of drought appear to have little effect on the saguaro's rate of fruit production (Thackery and Leding 1929, Steenbergh and Lowe 1977). The saguaro's year-to-year predictability and high productivity, when coupled with the timing of fruit production, suggest that the saguaro may represent a crucial water and nutrient source for many desert animals. Saguaros have been labeled keystone producers (Steenbergh and Lowe 1977).

In the Sonoran Desert, the congeneric White-winged (*Zenaida asiatica*) and Mourning (*Zenaida macroura*) Doves spend the summer breeding in the Sonoran Desert and their winters in Mexico and Central America. The White-winged Dove's breeding cycle appears to coincide with the reproductive cycle of the saguaro,

with White-winged Doves arriving in the Sonoran Desert of Arizona near the end of April when the saguaro flowers start blooming, and leaving in early September. Mourning Doves, in contrast, arrive earlier in the Sonoran Desert and breed later. Both species apparently require surface water for drinking every day or two, and may water more frequently during the hottest periods. Is the saguaro an important water and nutrient resource for White-winged and Mourning Doves? Does it provide a partial substitute for surface water for these species? Casual observations indicate that only the White-winged Dove makes overt use of the saguaro (Cunningham et al. 1997). The larger (144 ± 1.5 g; mean ± 1 SE, N = 89) White-winged Doves are often observed perched atop saguaros feeding on the flowers or fruit. In contrast, the somewhat smaller (110 ± 1.6 g, N = 56) Mourning Doves feed exclusively on the ground and do not appear to focus their foraging around saguaros. Both dove species are seed predators and have muscular gizzards that grind up the seeds that they ingest. How do these large differences in foraging mode and substrate use affect the importance of the saguaro as a source of water and nutrients for White-winged and Mourning Doves?

In this investigation we use a combination of stable isotope measurements of consumer tissues and body water and traditional dietary analysis: (1) to determine the importance of saguaro, relative to other desert plants, to the carbon budget of these desert-dwelling doves, and (2) to determine whether saguaro represents an important water resource for these birds. We use the distinct δ^{13}C and δD isotope values of saguaro fruit (Wolf and Martínez del Rio 2000) to examine the con-

tribution of this plant to the carbon and water budgets of two doves with contrasting foraging modes. We define foraging mode broadly to imply the repertoire of behaviors used to procure food. White-winged Doves are versatile foragers that feed on vegetation and on the ground on both fruits and seeds. Mourning Doves are seed eaters that feed on the ground.

Stable isotopes of carbon and nitrogen are often used to determine the flow of nutrients across ecological compartments. For example, Anderson and Polis (1998) and Ben-David et al. (1997) used stable isotope methods to assess the contribution of marine nutrient sources to island and riverine communities. The carbon isotope composition of consumer tissues reflects the isotope composition of food resources and has been used extensively to track nutrient flow and to identify dietary sources (Kelly 2000). Nitrogen, in contrast, enriches across trophic levels and provides insight into trophic position. Often, carbon and nitrogen isotope analyses are used in a complementary fashion to provide a two-dimensional picture of resource use in a group of consumers (Rosing et al. 1998). Here, we also show how complementary analyses of the carbon isotopes in consumer tissues and the hydrogen isotopes in body water can reveal the differing roles that a single resource can play in two closely related consumers.

METHODS

Study site

Research was conducted on lands within the U.S. Air Force Barry M. Goldwater Bombing Range (32°49′ N; 112°26′ W) in southern Arizona. This 10 797 km² area contains large undisturbed tracts of land isolated from agricultural areas. We chose a study site isolated from these areas because they could potentially provide doves with alternative food resources (C_4 agricultural crops) with carbon isotope values similar to those of the saguaro (CAM). The plant community on the study site is relatively undisturbed upland Sonoran Desert scrub (Turner et al. 1995). The flora has been described by Felger (1998). Although many species of cacti are present within the study area (e.g., *Echinocereus* spp., *Ferocactus* spp., *Mammillaria* spp., and *Opuntia* spp.), the doves ate only saguaro fruit.

Bird and crop contents collection

We collected (shot) White-winged and Mourning Doves weekly or biweekly from 30 April to 9 September 1998 (under U.S. Fish and Wildlife Service and Arizona Department of Game and Fish permits). Four to seven birds of each species were collected between 0700 and 1000 hours Mountain Standard Time (MST) on each sampling date. Immediately after collection, birds were placed in plastic bags and transported in ice to a laboratory freezer and held at −20°C at the University of Arizona. Within 10 d, carcasses were thawed and tissue samples (liver and pectoralis muscle) and

crop contents were collected. Crop contents were freeze-dried to constant mass and particles were then sorted according to plant species. Samples were weighed, to calculate the fraction of each plant species in the total crop contents. Seeds were identified using reference material from the University of Arizona's herbarium. We were able to identify 88% of the total species of plant material found in dove crops; for the 12% of unidentified seeds we ruled out cactus seeds and C_4 grasses from this group by looking at herbarium seed specimens of each species known to occur on the study area.

Sample preparation for isotope analyses

Water for δD analysis was extracted from dove pectoralis muscle by cryogenic vacuum distillation (Ehleringer 1989). Liver tissues (2–4 g) for carbon isotope analysis were freeze-dried to constant mass, defatted by petroleum ether extraction, and ground into a fine powder. Whole fruit pulp and pulp-free saguaro seeds were freeze-dried and ground into a fine powder for carbon isotope analyses. Water for δD analyses was extracted from fruit pulp by cryogenic vacuum distillation (Ehleringer 1989). In addition, we measured the carbon isotope composition of seeds from plant species (other than saguaro) that were frequently ingested by doves. These seeds were collected from plants in the field or obtained from the crops of birds we collected. We measured the $\delta^{13}C$ of seeds from six individual plants or several (four to six) dove crops. Seeds were dried and ground powder-fine for carbon isotope analyses.

Stable isotope analyses

Powdered plant and animal tissues (~0.15 mg) were loaded into precleaned tin capsules for isotope analysis. Carbon isotope ratios of plant and animal tissues were measured on a continuous flow isotope ratio mass spectrometer (VG Isotech, Optimia, Champaign, Illinois) with samples combusted in a Carlo Erba NA 1500 elemental analyzer (CE Instruments, Milan, Italy) at the Columbia University Biosphere 2 stable isotope facility in Oracle, Arizona, USA. The precision of these analyses was ±0.3‰. Laboratory standards, vacuum oil ($\delta^{13}C$ = −27.5‰ VPDB [Vienna Pee Dee Belemnite Standard]) and ANU (Australian National University) sucrose ($\delta^{13}C$ = −10.5‰ VPDB, NIST 8542) were included on each run in order to make corrections to raw values obtained from the mass spectrometer. Hydrogen isotope ratios were measured using a dual inlet isotope ratio mass spectrometer (Delta S, Finnigan MAT, San Jose, California) fitted with gas preparation Finnigan HD autosampler device at the stable isotope facility in the Geosciences department at the University of Arizona. The precision of these analyses was ±0.5‰. Laboratory standard waters were calibrated against the international standards GISP (Greenland Ice Sheet Project) and VSMOW (Vienna Standard Mean

Ocean Water) and run with samples to provide corrections.

Stable isotope ratios were expressed using standard delta notation (δ) in parts per thousand (‰) as

$$\delta X = (R_{sample}/R_{standard} - 1) \times 1000$$

where R_{sample} and $R_{standard}$ are the molar ratios of $^{13}C/^{12}C$ or $^2H/H$ of the sample and the reference standard, respectively. Samples were referenced against international standards, VPDB for carbon and VSMOW for water.

Estimation of the incorporation of saguaro carbon into dove tissues

We estimated the proportion of a dove's diet that was derived from saguaro by using a two-end-point mixing model (Kline et al. 1990, Gannes et al. 1997):

$$\delta^{13}C_{liver} = p(\delta^{13}C_{saguaro}) + (1 - p)(\delta^{13}C_{C_3}) + \Delta$$

in which p is the fraction of saguaro in the diet that is incorporated into the focal tissue and Δ is the apparent discrimination factor, estimated at 0.3‰ (Hobson and Clark 1992a). The apparent discrimination factor is defined as the difference in isotope composition between tissues and diet when animals are feeding on a pure diet (DeNiro and Epstein 1978, Hobson and Clark 1992a, Cerling and Harris 1999). The carbon isotope ratio of saguaro products used in these calculations was $\delta^{13}C_{saguaro} = -13.1$‰ VPDB when birds were feeding on fruit (Wolf and Martínez del Rio 2000). The $\delta^{13}C$ values of pulp without seeds and pulp-free seeds did not differ significantly (paired $t = 0.37$, $P > 0.5$, $N = 9$). The average $\delta^{13}C$ value used for C_3 plants was $\delta^{13}C_{C_3} = -24.9$‰ VPDB. The carbon isotope composition of C_3 seeds consumed by doves was remarkably constant (coefficient of variation = 3.3%) and allowed us to use a single C_3 value in our two-point mixing model (Wolf and Martínez del Rio 2000).

We chose to analyze the isotope composition of liver tissue because Hobson and Clark (1992a) suggest that its apparent discrimination factor is minimal in birds and because this tissue provides a period from ingestion to tissue incorporation that is relatively short. Diet-to-tissue fractionation in liver is small in other granivorous birds, ~0.3‰ (Hobson and Clark 1992a), and the carbon half-life of liver tissue in quail is ~2.5 d (Hobson and Clark 1992b).

RESULTS

Resource use as described by crop content analysis

White-winged Doves began feeding on saguaro fruit as soon as it became available in mid-June and continued eating it until early September (Fig. 1A). At the end of August several birds still had saguaro fruit in their crops, although we were unable to find saguaro fruit ourselves in a search over a very large area (Wolf and Martínez del Rio 2000). White-winged Doves were
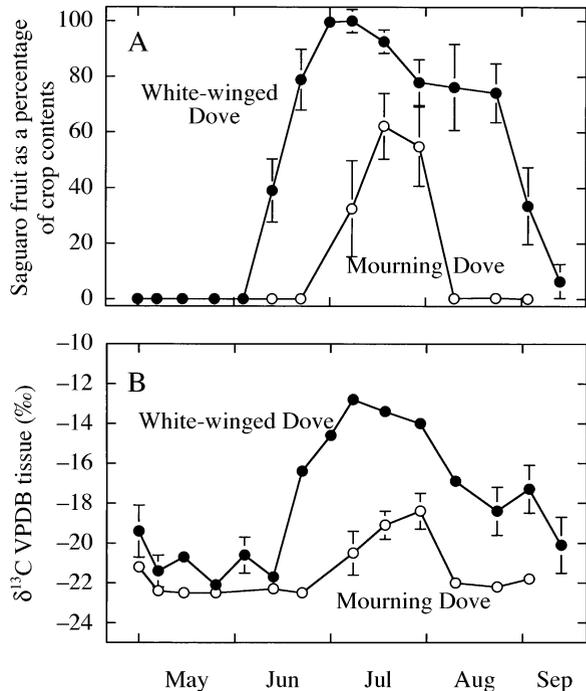

FIG. 1. (A) Temporal changes in the percentage of saguaro in White-winged and Mourning Dove crop contents. (B) Temporal changes in the carbon isotope composition ($\delta^{13}C$) of dove liver. Note the correspondence between diet and isotope composition. Points are means, and bars indicate ±1 SE (N ranged from 4 to 10 individuals).

more proficient at finding saguaro fruit than we were. Saguaro fruit accounted for >50% of the diet of White-winged Doves from June to August (Fig. 1A). In July, at the peak of saguaro availability, White-winged Doves specialized on saguaro and saguaro fruit comprised >90% (91 ± 15% [mean ± 1 SD], $N = 17$ individual dove crops) of the dry mass of their crop contents. Saguaro was the most abundant and the most frequently encountered plant in White-wing Dove diets (Fig. 2). Averaged over the entire season, saguaro fruit accounted for over half (55 ± 44%, $N = 81$ individual dove crops) of White-winged Dove crop contents.

Mourning Doves were less dependent on saguaro than White-winged Doves. Between May and September, saguaro seeds accounted for only 14 ± 28% ($N = 61$ individual dove crops) of the dry matter in their diet (Fig. 1A). However, during July, at the peak of saguaro production, saguaro seeds represented slightly under half (48.5 ± 35%, $N = 17$ individual dove crops) of Mourning Dove crop contents. White-winged and Mourning Doves differed in how they harvested saguaro fruit and in what materials they obtained from it. We frequently observed White-winged Doves feeding on top of saguaros. In contrast, although Mourning Doves often fed on the ground at the base of saguaro cacti, we never observed them feeding on top of the plants. Of the 53 White-winged Doves collected that
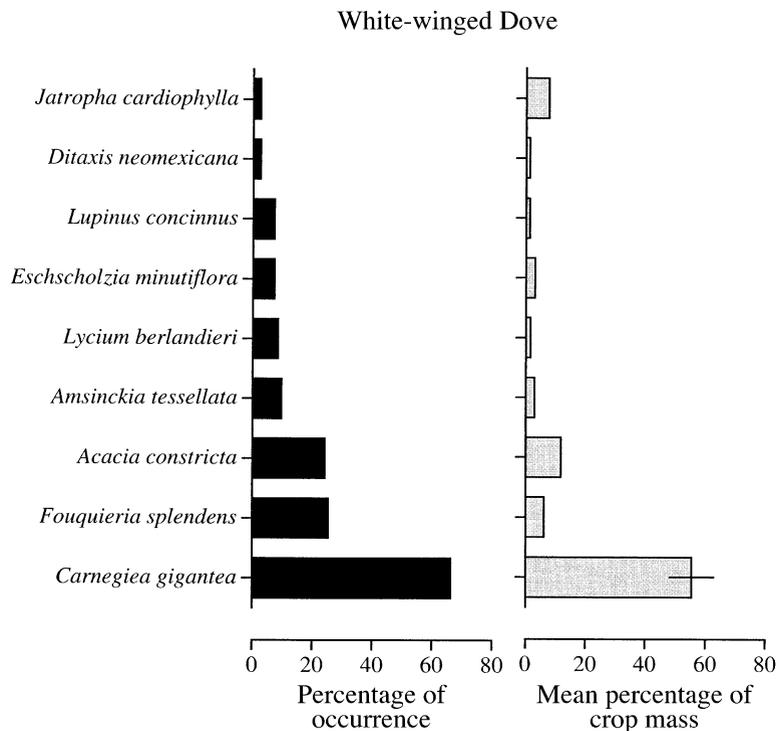
White-winged Dove

FIG. 2. Summer diet (crop contents) of White-winged Doves. Standard errors, except for *Carnegiea gigantea*, are too small to see. Saguaro was the most frequently encountered and abundant item in the diet of White-winged Doves.

had saguaro fruit in their crops, 28 (53%) had both seeds and fruit pulp, whereas 25 had exclusively seeds. Mourning Doves avoided pulp and fed almost exclusively on seeds. Twenty-three of the 24 Mourning Doves that had saguaro in their crops had only seeds.

White-winged Doves and Mourning Doves also differed in the species of seeds that they ingested in addition to saguaro. Perennial plants such as *Acacia constricta*, *Fouquieria splendens*, and *Lycium berlandieri* figured most prominently in the diet of White-winged Doves (Fig. 2). Mourning Doves fed primarily on winter annuals such as *Eschscholzia minutiflora*, *Amsinckia tessellata*, and *A. intermedia* (Fig. 3).

Use of saguaro fruit as revealed by stable isotope analyses

The carbon isotope signatures of saguaro fruit pulp were typical of plants with CAM photosynthesis ($\delta^{13}C$ = $-13.1 \pm 0.3‰$, $N = 28$ saguaro fruit samples). The carbon isotope ratio of saguaro fruit was temporally stable and distinct from other plant resources used by White-winged and Mourning Doves (Wolf and Martínez del Rio 2000). Excepting saguaro, the seeds and fruit found in the crops of both White-winged and Mourning Doves were from plant species with C_3 photosynthesis (Wolf and Martínez del Rio 2000). The average $\delta^{13}C$ of C_3 plants making up the majority of non-saguaro items in the doves' diet was $-24.9 \pm 0.3‰$

VPDB (ranging from -23.9 to $-25.9‰$, $N = 6$ plant species).

The water contained in saguaro fruit pulp also had distinctive hydrogen isotope values relative to those of available surface water. The δD of saguaro fruit during the sampling period averaged $48.4 \pm 1.6‰$ VSMOW ($N = 82$ saguaro fruit samples) and did not vary significantly with time (ANOVA, fruit, $F_{2,75} = 1.02$, $P = 0.37$, $N = 77$ saguaro fruit samples). In contrast, evaporative enrichment resulted in an increase in deuterium isotope composition of water contained in the Arizona Game and Fish water catchments used by doves (from -37.3 to $-23.5‰$ VSMOW, from mid-May to 30 June). Monsoon rains, starting in July, periodically refilled catchments with water that was depleted in deuterium compared to basin 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.

From the end of April to the middle of June, White-winged Doves maintained a relatively constant fraction of CAM/C_4 based carbon in their livers. During this period, liver $\delta^{13}C$ averaged $-20.9 \pm 1.9‰$ VPDB ($N = 31$ individual dove liver samples). The onset of saguaro fruit availability in mid-June was accompanied by a rapid increase in the $\delta^{13}C$ of dove liver tissues, which remained high (>50% incorporation) through the end of August (Fig. 1B). Because the percentage
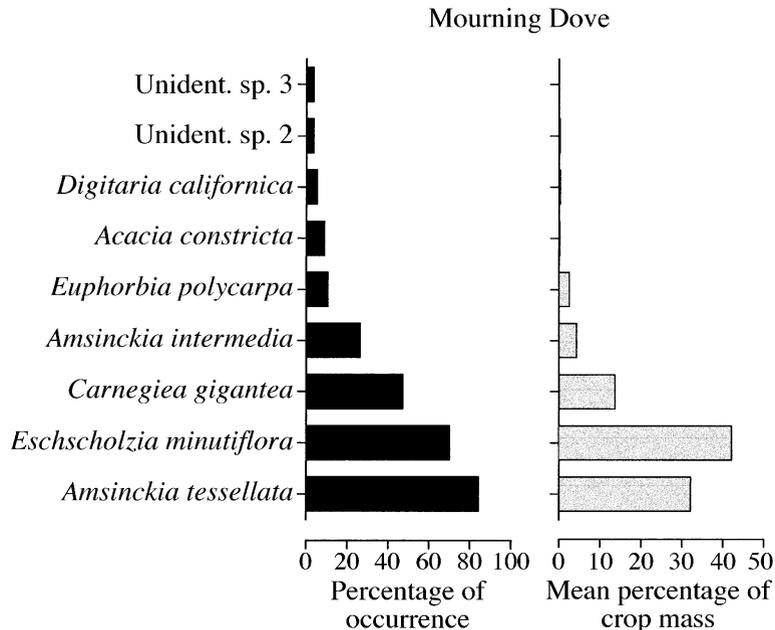
Mourning Dove

FIG. 3. Summer diet (crop contents) of Mourning Doves, shown as percentage of occurrence of the plants in the diet, and as mean percentage of dry mass.

of saguaro in crop contents and the carbon isotope $\delta^{13}C$ of liver tissue were linearly and positively correlated ($r = 0.75$, $P < 0.001$, $N = 81$ individual dove liver samples), the carbon incorporation curve roughly tracked percentage of saguaro in crop contents (Fig. 1B). The carbon isotope signature of dove liver tissues provided a picture of saguaro use similar to that delineated by crop contents. During June, after the onset of saguaro fruit availability, stable isotope analyses revealed that $84 \pm 11\%$ ($N = 18$ individual dove liver samples) of the carbon in dove livers was derived from saguaro fruit. During July, August, and September, stable isotope measurements indicated that saguaro comprised $92 \pm 24\%$ ($N = 17$ individual dove liver samples), $64 \pm 21\%$ ($N = 18$ such samples) and $42 \pm 28\%$ ($N = 6$ such samples), respectively, of the incorporated carbon in the tissue of White-winged Doves. Overall, from the onset of fruit availability in mid-June through August, saguaro fruit accounted for $80 \pm 22.4\%$ ($N = 53$ individual dove liver samples) of incorporated carbon. Averaged over the entire sampling period, carbon isotope data indicate that saguaro or C_4 plants accounted for $62 \pm 30\%$ ($N = 90$ individual dove liver samples) of the total carbon incorporated into White-winged Dove liver tissue.

During May, June, and August, Mourning Dove liver tissues had a stable carbon isotope signature that averaged $-22.2 \pm 0.7‰$ VPDB (range -20.2 to $-23.1‰$, $N = 43$ individual dove liver samples). The $\delta^{13}C$ of Mourning Dove liver tissue varied significantly among June, July, and August ($F_{2,38} = 19.6$, $P < 0.001$). July $\delta^{13}C$ tissue values were significantly more positive than those found in June and August (Tukey-Kramer hsd

test, $P < 0.05$), which did not differ significantly (Tukey-Kramer hsd test, $P > 0.05$). In July, $47 \pm 18\%$ ($N = 17$ individual dove liver samples) of the carbon in Mourning Dove livers was derived from saguaro seeds (Fig. 1B). The $\delta^{13}C$ of liver tissue was linearly and positively correlated with the percentage of saguaro seeds in Mourning Dove crops ($r = 0.89$, $P < 0.001$, $N = 55$ individual dove crops), and thus the temporal changes in $\delta^{13}C$ paralleled changes in percentage of saguaro seeds in crop contents (Fig. 1A, B).

The deuterium composition of White-winged Dove body water tracked saguaro utilization (Wolf and Martínez del Rio 2000). Indeed, in White-winged Doves the δD in body water and the percentage of saguaro in crop contents were positively and linearly correlated ($r = 0.75$, $P < 0.001$). In addition, in White-winged Doves $\delta^{13}C$ and δD were significantly correlated ($r = 0.82$, $P < 0.001$, $N = 91$ individual doves, Fig. 4A), indicating that saguaro water and carbon were incorporated concurrently into the doves' body water and tissues. In contrast, in Mourning Doves an increase in the percentage of saguaro seeds in the crop was not accompanied by an increase in δD of the body water ($r = 0.11$, $P > 0.1$, $N = 55$), and these birds exhibited no significant correlation between $\delta^{13}C$ and δD ($r = 0.08$, $P > 0.5$, Fig. 4B). Although Mourning Doves incorporated a significant amount of saguaro carbon into their tissues in July, they incorporated little if any saguaro water.

DISCUSSION

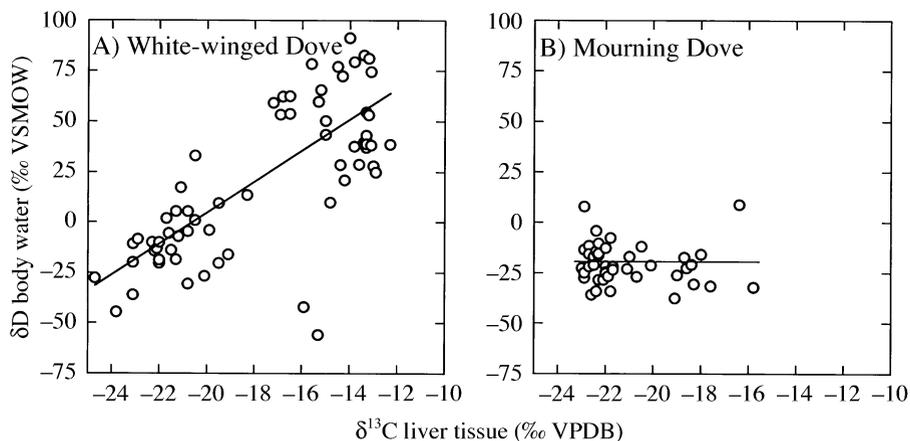The nutrients and water contained in saguaro fruit have distinctive carbon and deuterium isotope ratio val-

FIG. 4. Relationship between carbon isotope composition in liver ($\delta^{13}C$) and hydrogen composition in body water (δD) in (A) White-winged Doves and (B) Mourning Doves. Note that in White-winged Doves $\delta^{13}C$ and δD are positively correlated ($r = 0.82$, $y = 7.7x + 158.7$, $P < 0.001$), whereas in Mourning Doves they are not ($r = 0.11$, $P > 0.55$, $\delta D = 18.4 \pm 15$ [mean $\pm$ 1 SD], $N = 60$).

ues compared to other resources in the environment. Thus, saguaro fruit provides the unusual opportunity of allowing an independent assessment of its importance as both a water and nutrient source to consumers. Temporal changes in the isotopic composition of the tissues of White-winged and Mourning Doves revealed strong differences in the intensity of saguaro utilization by each species (Fig. 1B). In addition, our analysis revealed that the two species obtained a contrasting combination of resources from the saguaro's fruit. White-winged Doves, which perched on and fed from the intact fruit, were saguaro specialists (sensu Sherry 1990), and obtained both nutrients and water from this resource (Fig. 4A). Mourning Doves, in contrast, obtained only the nutrients contained within saguaro seeds (Fig. 4B). This result was a consequence of their foraging behavior; Mourning Doves fed only on seeds, including those of the saguaro, from the ground. The larger White-winged Doves, however, are highly frugivorous and fed on seeds both on the ground and when perched in saguaros and other trees and shrubs.

Isotopic analyses complement traditional crop content analysis because they provide evidence that what is eaten by an animal is actually assimilated and incorporated into its tissues (Gannes et al. 1997). This study highlights the reciprocal importance of complementing isotopic analyses with traditional detailed crop content data. Our analysis of crop contents not only supported the conclusions of our isotopic analyses, it also provided a mechanism that explained its most important result: saguaro fruit was differentially used as a source of nutrients and water by two avian consumers. Crop content data revealed that White-winged Doves often ingested saguaro pulp and seeds, whereas Mourning Doves ingested only seeds. Most of the water in saguaro fruit is found in its juicy pulp, which is ~75% water by mass (Wolf and Martínez del Rio 2000). Saguaro seeds alone are relatively dry and contain only

~6.5% water by mass (Greene 1936). Stable isotopes revealed that White-winged Doves acquired both carbon and water from saguaro pulp, whereas Mourning Doves acquired only carbon from saguaro seeds (Fig. 4).

Crop contents data provided additional insight into the foraging ecology of these two dove species. When not feeding on saguaro, White-winged Doves typically harvested the seeds and fruits of large-seeded perennials such as *Fouqueria splendens*, *Acacia constricta*, *Jatropha cardiophyla*, and *Lycium berlanderi* while perching on the plants (Fig. 2; Wolf and Martínez del Rio 2000; R. A. Haughey, *unpublished data*). In the Sonoran Desert of Arizona, we consider White-winged Doves to be frugivorous granivores. Mourning Doves, in contrast, were strictly granivorous (Cunningham et al. 1997) and most frequently picked the small seeds of desert annuals such as *Amsinckia tessellata*, *A. intermedia*, and *Eschscholzia minutiflora* from the ground (Fig. 3). Seeds from the perennial plants typically harvested by White-winged Doves were, on average, 20 times heavier than the annual plant seeds harvested by Mourning Doves. Because uneaten saguaro fruit dries and falls to the ground as a solid sticky mass of pulp and seeds, it is unlikely that Mourning Doves fed primarily on fallen fruit. Casual observations suggest that Mourning Doves take advantage of the abundant "second harvest" of saguaro seeds defecated by both birds and mammals (Felger and Moser 1985, Haughey 1986, Wolf and Martínez del Rio 2000). We use the term second harvest in analogy of the name used for the practice of some Seri Indian bands of Sonora. These peoples ingested saguaro fruit, collected their own feces, sieved them to recover the undigested seeds, washed the seeds, and then ground them into a nutritious mush, which they ate (Felger and Moser 1985).

Saguaro fruit possesses a distinctive carbon isotope signature that is rapidly and faithfully incorporated into

the tissues of its consumers. Indeed, in both White-winged and Mourning Doves there was a significant positive correlation between the percentage of saguaro material found in the crop and liver δ^{13}C. Wolf and Martínez del Rio (2000) have used this signature to estimate the flux of carbon, and hence energy, from saguaros into doves. Briefly, Wolf and Martínez del Rio (2000) used seasonal changes in tissue δ^{13}C of White-winged Doves to estimate the fraction of a dove's energy budget that was derived from saguaro. Integration of the product of this fraction and the dove's rate of energy use over time yielded an estimate of the seasonal contribution of saguaro to the energy budget of a White-winged Dove (Wolf and Martínez del Rio 2000). Making a quantitative estimate of energy flux hinges crucially on knowledge about the faithfulness with which the isotope value of a source is incorporated into a consumer's tissues. The small discrimination factor between saguaro fruit and dove liver tissue suggested by Hobson and Clark's (1992a) work facilitated Wolf and Martínez del Rio's (2000) analyses.

Can a similar procedure be used to estimate the contribution of saguaro to the water budget of White-winged Doves? Maybe, but doing so will require a better understanding of the processes that lead to discrimination between water sources and body water. As Wolf and Martínez del Rio (2000) point out, the discrimination factor that accompanies the incorporation of saguaro water into the dove's body water is unknown, it is likely to be high, it may be variable, and it probably depends on environmental conditions such as environmental temperature and relative humidity. Note that in Fig. 4A the δD of White-winged Dove body water at the peak of saguaro use is greater than δD in saguaro fruit water. Note also that the isotope composition of Mourning Dove body water was more positive than that of the surface water that they used (Fig. 4B). The δD enrichment that doves exhibit probably results from fractionation during cutaneous and respiratory water losses (Wolf and Martínez del Rio 2000). At present, this phenomenon allows only a qualitative assessment of the importance of saguaro as a water resource for doves. Further research into the dynamics of water transfer and isotopic fractionation are needed to support a more quantitative assessment. Thus, our current data allow the limited assertion that saguaro fruit is a major contributor to the water budgets of White-winged Doves, but that it does not contribute to the water budgets of Mourning Doves.

These observations suggest that the presence of saguaros in the Sonoran Desert provide White-winged Doves with a water source that is unused by Mourning Doves. On our study site, where saguaro densities range from 20 to 60 plants/ha, there appears to be no direct competition among dove species for saguaro fruit. Saguaro fruit are superabundant from mid-June until the middle of July. The water requirements of both doves are high during this period because evaporative cooling

is the only means of heat dissipation when environmental temperatures exceed body temperature (Wolf 2000). In addition, these high environmental temperatures demand that doves cool their eggs during incubation to maintain viability. Doves cool their eggs by lowering their body temperature through cutaneous and respiratory evaporation (Walsberg and Voss-Roberts 1983). Finally, after hatching, adults feed young crop milk, a nutritious fluid that is produced by the sloughing of the gastrointestinal epithelium (Cottam and Trefethen 1968). Crop milk production further increases adult water requirements. With these high water requirements, the current widespread distribution of the Mourning Dove in the Sonoran Desert during the summer may be an artifact of the significant effort by the Arizona Game and Fish Department to provide water for big game animals throughout the year.

The numerous big game water catchments that the Game and Fish Department has installed provide reliable water resources for doves throughout the hotter portions of the Sonoran Desert north of the border between the U.S. and Mexico. In most places there is a catchment within a 10–20 km radius (D. Urquidez, Arizona Game and Fish Department, *personal communication*). Thus, strong-flying birds such as White-winged and Mourning Doves have access to surface water. These constructed surface water resources probably allow Mourning Doves to breed in almost all regions of the Sonoran Desert north of the U.S.–Mexico border. We speculate that the presence of saguaros reduces the reliance of White-winged Doves on surface water. Before the construction of water catchments, the contribution of saguaro to the water economy of White-winged Doves may have allowed them to occupy areas where water was only sporadically available and where Mourning Doves were absent. This hypothesis is testable; south of the U.S.–Mexican border, the Sonoran Desert contains few constructed water catchments. We predict that this region contains breeding populations of White-winged Doves, but no breeding Mourning Doves.

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