

WATER ECONOMY AND SALT BALANCE IN WHITE-WINGED AND INCA DOVES

RICHARD E. MACMILLEN AND CHARLES H. TROST

Two of the most conspicuously abundant birds during the summer in the Sonoran desert regions of southern Arizona and northern Mexico are White-winged Doves (*Zenaida asiatica*) and Inca Doves (*Scardafella inca*). These doves have nearly identical general distributions extending over arid parts of the southwestern United States and south through Mexico into Central America. However, within this range Inca Doves are confined to desert towns and villages while White-winged Doves occur throughout the deserts (Ridgway, 1916; Bent, 1932). In addition there are seasonal differences in distribution at least within the United States, with the strong-flying White-winged Doves represented only as spring and summer residents while the relatively sedentary Inca Doves are continuously resident (Bent, 1932).

In their enlightening review article on the water economy of land birds, Bartholomew and Cade (1963) indicate an apparent direct relationship between body weight and efficiency of osmotic homeostasis. The differences in body weight between White-winged Doves (*ca.* 140 g) and Inca Doves (*ca.* 40 g), together with differences in habitat preference and mobility in the same desert macroenvironment, afforded an excellent opportunity to test the proposed relationship between body weight and water economy in two closely related land birds.

Therefore, this study undertakes to examine the water relations of White-winged and Inca doves in light of taxonomic affinity, similarity of macroenvironment, and differences in body size, mobility, and micro-environmental preferences.

MATERIALS AND METHODS

The 17 White-winged Doves and 27 Inca Doves used were all collected in or near Tucson, Pima County, Arizona, between September, 1964, and August, 1965. The birds were shipped by air to California, invariably arriving in the laboratory in excellent condition within 24 hours of initial departure. Because of their migratory habits, White-winged Doves were shipped only in the spring and summer months, while Inca Doves were available throughout the year.

All birds were placed in a large roof-top aviary, thus subjected to natural photoperiod and ambient conditions, and provided in excess with tap water and mixed bird seed. During all phases of experimentation the birds were housed in a windowless room on a 12-hour photoperiod (lights on from 1000 to 2200 hours) with ambient temperature and relative humidity fluctuating between 20–24°C and 35–50 per cent, respectively. The experimental period extended from September, 1964, to November, 1965. Except for the studies of salinity discrimination and utilization of succulent foods, the birds were housed individually in cages measuring

51 × 25.5 × 25.5 cm (White-winged Doves) or 25.5 × 25.5 × 25.5 cm (Inca Doves); each cage was equipped with an inverted graduated cylinder bearing an L-shaped drinking tube for measuring fluid intake. During all phases of this study the birds were provided in excess with mixed bird seed for food, which contained between 9 and 10 per cent water by weight. Only adult birds were used and no attempt was made to segregate the birds according to sex.

Ad-libitum intakes of tap water and various dilutions of sea water were measured daily to the nearest 0.5 ml, just prior to the end of the dark period; an additional drinking device was employed as a control to measure evaporation. Various dilutions of sea water were made with distilled water; sea water (salinity 33 ppt) was obtained from Marineland of the Pacific, Palos Verdes, California. The birds were weighed to the nearest 0.1 g at the end of the dark period on Mondays, Wednesdays, and Fridays. Unless otherwise specified all tests were run for seven days, and the birds were provided with intervening periods of tap-water drinking between the various sea-water regimens. We soon determined that the White-winged Doves could not be induced to drink sufficient quantities of the more concentrated but still tolerable sea-water dilutions unless they had been deprived of drinking water for two or three days. After prior water deprivation the birds commenced and continued to drink large quantities.

Minimal requirements of tap water and of sea-water dilutions were determined by progressively restricting the daily ration of each tolerable drinking solution until that amount was found below which the birds could not maintain weight. During the studies of minimal water requirements the birds were weighed daily at the end of the dark period.

Blood was collected for measurements of the plasma osmotic pressure and chloride at the end of each *ad-libitum* drinking experiment. The blood was removed (0.8 ml from White-winged Doves, 0.5 ml from Inca Doves) with heparinized (rinsed, then dried) 1.0 ml syringes from the brachial vein for osmotic pressure determinations; blood for chloride measurements was drawn up in heparinized capillary tubes from the syringe puncture. The blood samples were centrifuged for five minutes, after which the plasma was removed. Plasma osmotic pressure was determined with a Mechrolab Vapor Pressure Osmometer; sufficient plasma for analysis could be obtained from the White-winged Doves without dilution, but the plasma of Inca Doves was diluted with glass-distilled water in order to obtain sufficient amounts for measurement. Plasma chloride concentrations were measured in both species without dilution, using an Aminco-Cotlove Chloride Titrator.

The effects of water deprivation on body weight and survival were determined for five birds of each species by depriving them of drinking water following a period of tap-water hydration. The birds were provided with mixed bird seed in excess for food and were weighed daily until death.

The tests of salinity discrimination were conducted in a cage containing five birds and measuring 43.5 × 61 × 76.5 cm. Four drinking devices were arranged in the cage at 90° intervals on a ring stand. The two solutions to be tested were put in alternate drinking devices and the ring stand was rotated 90° daily to minimize the use of clues other than taste. Each test was of seven days duration and the White-winged Doves and Inca Doves were tested separately.

In assessing the utilization of succulent foods as a water source five birds of each species were housed, each species separately, in a cage measuring 43.5 × 61 × 76.5 cm. Well-hydrated birds were deprived of drinking water and provided with succulent food (fresh, halved tomatoes, chopped lettuce, or *Tenebrio* larvae) together with mixed bird seed. In addition, since White-winged Doves were observed in Arizona

making extensive use of saguaro cactus (*Cereus giganteus*) fruit, both species were provided in the laboratory with ripe fruit of the most readily obtained substitute, prickly pear cactus (*Opuntia occidentalis*). The birds were weighed daily.

RESULTS

Body weights.—The means and standard deviations of initial body weights of the 17 White-winged and the 27 Inca doves were mean 140.3, SD 19.5 g, and mean 41.0, SD 2.7 g, respectively. These weights were those of each bird just prior to its use indoors as an experimental subject. While drinking tolerable solutions the experimental birds remained in excellent health and generally gained weight.

Ad-libitum water intake.—The mean responses to *ad-libitum* drinking by White-winged Doves to the various drinking solutions are shown in Figure 1. On tap water 10 birds drank 12.4 (sd 7.0) per cent of their body weight per day; in birds on the sea-water dilutions and those forced to drink by prior water deprivation, *ad-libitum* drinking tended to increase

Zenaida asiatica

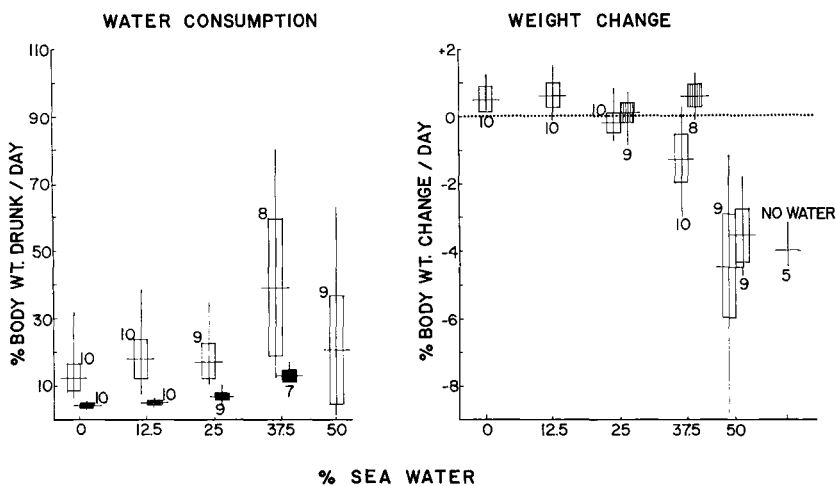


Figure 1. Daily water consumption and weight changes of White-winged Doves on various dilutions of sea water. Vertical lines indicate ranges. Horizontal lines indicate means (\bar{X}). Rectangles inclose the interval $\bar{X} \pm 2$ SE. Numbers represent sample sizes. In the graph of water consumption, hollow rectangles indicate *ad-libitum* data, and filled rectangles indicate minimal water requirements. In the graph of weight changes, hollow rectangles indicate data from birds not experiencing prior dehydration, and filled rectangles indicate prior-dehydration data.

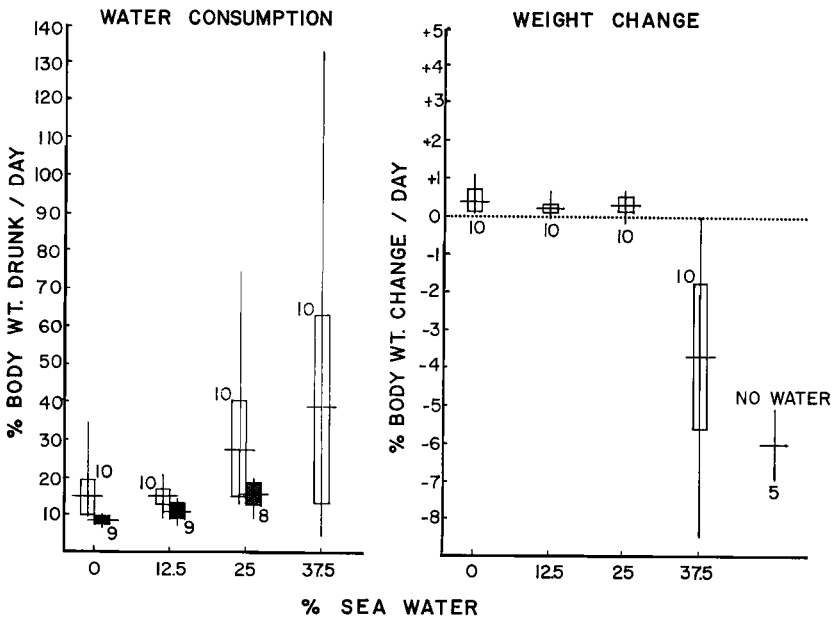
Scardafella inca

Figure 2. Daily water consumption and weight changes of Inca Doves on various dilutions of sea water. Symbols as in Figure 1.

with concentrations through 37.5 per cent sea water but decreased on 50 per cent sea water. Because of large individual differences in water intake on the various drinking solutions, only the consumptions of tap water and of 37.5 per cent sea water were significantly different. Figure 1 also demonstrates the mean responses of body weight in White-winged Doves to the drinking solutions, as well as the relative palatability of these solutions. The birds maintained weight on both tap water and 12.5 per cent sea water but, unless forced to drink by prior water deprivation, they lost weight on higher concentrations. However, if White-winged Doves were deprived of water in advance for several days they maintained weight on 25 per cent sea water and gained weight on 37.5 per cent sea water. Neither well-hydrated nor dehydrated birds maintained weight while drinking 50 per cent sea water; both lost weight at about the same rate as when they were deprived of water altogether (Figure 1). On each regimen resulting in weight loss, the mean daily loss was significantly greater than that on the next less concentrated saline drinking solution.

In Inca Doves mean daily *ad-libitum* drinking of tap water and of 12.5

Zenaida asiatica - PLASMA

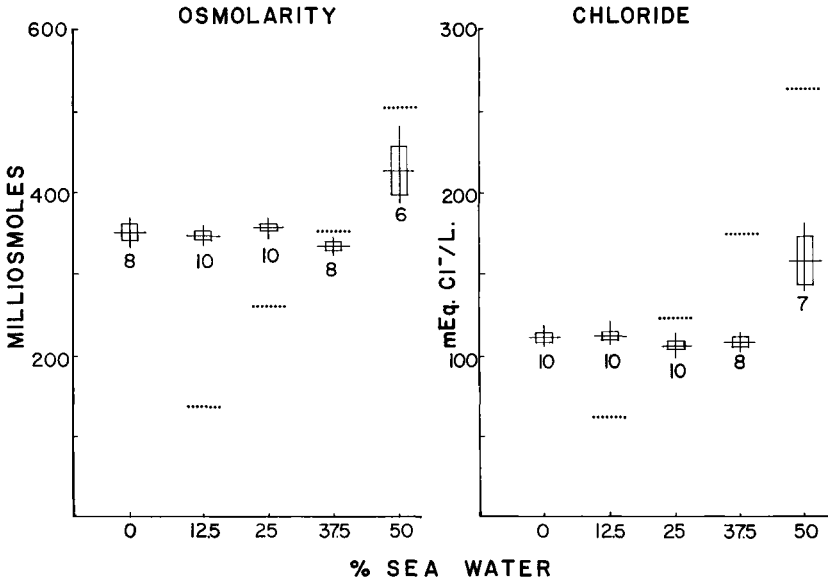


Figure 3. Plasma osmolarities and chlorinities in White-winged Doves while drinking various sea-water dilutions. The dotted lines indicate the osmolarities and chlorinities of the respective drinking solutions. Other symbols as in Figure 1.

per cent sea water was essentially the same (14.6, SD 7.6, and 14.8, SD 3.5 per cent of body weight, respectively); on 25 and 37.5 per cent sea water both mean daily drinking and individual variation increased with concentration (Figure 2). Because of this increase in drinking variability there were no significant differences between mean daily *ad-libitum* water intakes. Since Inca Doves drank freely of whatever drinking solutions were offered, prior dehydration was not necessary. Mean daily gains in body weight occurred while drinking tap water, 12.5, and 25 per cent sea water; Inca Doves lost weight rapidly while drinking 37.5 per cent sea water, but at a lower rate than when water was withheld altogether (Figure 2).

Minimal water requirements.—The data on minimal daily water requirements for both White-winged and Inca doves are summarized in Figures 1 and 2. In both species the minimal water requirements and individual variations increased directly with concentration. The minimal daily rations for White-winged Doves were invariably significantly different from their *ad-libitum* daily intakes on each tolerable drinking solution, averaging

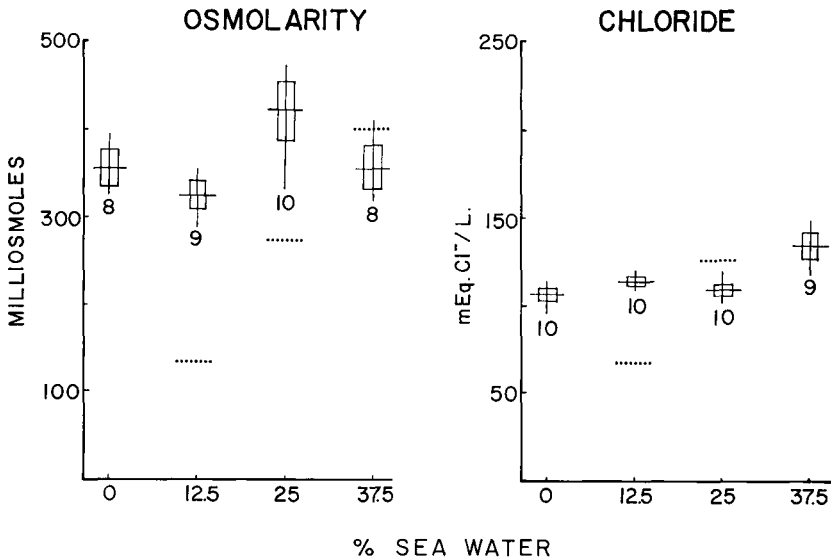
Scardafella inca - PLASMA

Figure 4. Plasma osmolarities and chlorinities in Inca Doves while drinking various sea-water dilutions. Symbols as in Figure 3.

around one-third to one-half of the *ad-libitum* amounts. The minimal daily water requirements of Inca Doves were only slightly and generally insignificantly lower than their *ad-libitum* amounts, varying between about 70 and 80 per cent of the latter. Relative to weights, daily minimal intakes of the smaller Inca Doves were about twice those of the White-winged Doves on the same drinking regimens.

Plasma osmotic pressure.—While drinking *ad-libitum* solutions upon which weight could be maintained, plasma osmotic pressure of White-winged Doves remained reasonably stable with means varying from 353.2 (SD 13.1) mOs on tap water to 335.4 (SD 6.7) mOs on 37.5 per cent sea water (Figure 3). The greatest disparity in plasma osmotic pressure while on tolerable drinking solutions occurred between birds drinking 25 per cent and 37.5 per cent sea water, with mean values of 357.5 (SD 6.5) and 335.4 (SD 6.7) mOs, respectively. This disparity is probably caused by the differences in experimental procedures used in the two samples: plasma from the doves drinking 25 per cent sea water was removed from birds which had not experienced dehydration prior to receiving the drinking solution, and hence had shown a slight net loss in body weight indicating

WEIGHT LOSS

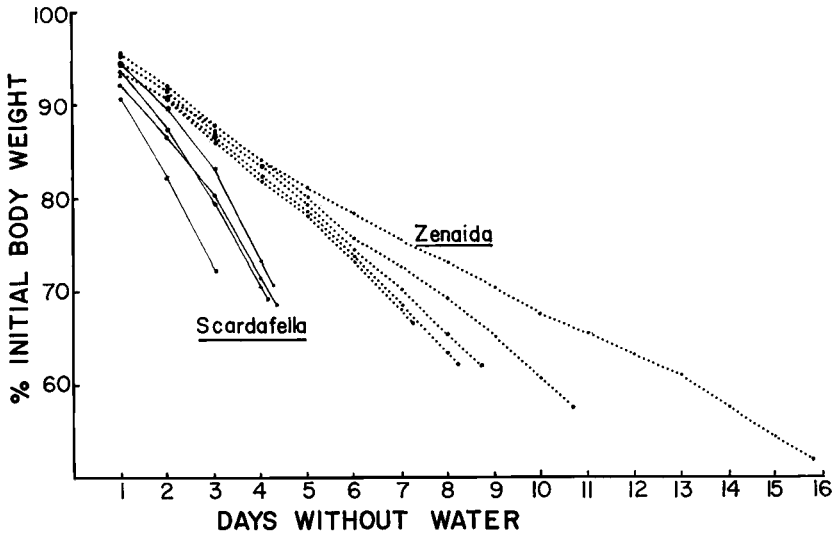


Figure 5. Changes in body weight in White-winged and Inca doves deprived of water until death (ends of lines). The dotted lines represent White-winged Doves and the solid lines represent Inca Doves; only a dot is used to denote one Inca Dove which died on the first day of water deprivation.

a condition of negative water balance; plasma was removed from birds gaining weight while drinking 37.5 per cent sea water after a period of prior dehydration (see Figure 1). The plasma osmotic pressure of birds gaining weight while drinking 37.5 per cent sea water is hypo-osmotic to the drinking solution (335.4 vs. 354.6 mOs). While drinking 50 per cent sea water, a hyper-osmotic solution upon which weight could not be maintained under any circumstances, White-winged Doves had significantly elevated plasma osmotic pressures (mean, 428.4, SD 32.6 mOs), indicating a partially dehydrated state (Figure 3).

In Inca Doves the plasma osmotic pressures, over the range of drinking solutions tested, were extremely variable (Figure 4). We think that this variability is a result, at least in part, of our routine use of often rather extreme dilutions of the plasma samples (as great as 10 : 1) to facilitate measurement. We suspect that sufficient error was thus introduced that an analysis of the differences in plasma osmotic pressure would be impractical. However, the data should be sufficiently reliable to allow a comparison of plasma osmotic pressure values between Inca Doves and White-winged Doves. The combined mean plasma values for White-winged

TABLE 1
EFFECTS OF WATER DEPRIVATION AND REHYDRATION ON WHITE-WINGED AND INCA DOVES¹

<i>Measurement</i>	<i>Species</i>	
	Zenaida asiatica	Scardafella inca
Water deprivation		
Days to death		
Minimum	7.5	1.0
Mean	10.2	3.8
Maximum	15.5	5.0
Mean per cent initial body weight		
At death	60.3	73.3
Lost per day	4.0	6.1
Rehydration		
Water consumption, normally hydrated		
<i>Ad libitum</i> , mean per cent body weight drunk per day	12.4	14.6
Minimal, mean per cent body weight drunk per day	4.2	8.5
Water consumption, after mild dehydration		
First 5 minutes, mean per cent body weight drunk	18.0	12.4
First 60 minutes, mean per cent body weight drunk	21.0	15.3
Weight change, per cent initial body weight		
After mild dehydration	79.7	82.2
After first 60 minutes of rehydration	95.5	92.7

¹ In all instances 5 birds were used, except that 10 Inca Doves were used in rehydration studies.

Doves and Inca Doves while drinking tap water through 37.5 per cent sea water are 348.4 and 364.3 mOs, respectively.

Plasma chlorinity.—In White-winged Doves the plasma chloride values remained fairly stable while the birds were on tolerable drinking solutions (tap water through 37.5 per cent sea water). The only noteworthy discrepancy was that shown by birds losing weight slightly (as explained above) on 25 per cent sea water; this value was generally lower than the others, and significantly lower than that of birds on 12.5 per cent sea water (Figure 3). The combined mean plasma chlorinities from birds drinking tolerable saline solutions was 109.7 mEq/l. In birds drinking but losing weight on 50 per cent sea water, the mean plasma chloride level (158.5 mEq/l, sd 17.8) was considerably and significantly elevated over those on other drinking regimens.

Inca Doves likewise had rather stable plasma chlorinities while drinking tolerable solutions (tap water through 25 per cent sea water), and similarly responded to a more concentrated drinking solution (37.5 per cent sea water) with significantly increased plasma levels (Figure 4). The combined mean plasma chlorinity of birds on tolerable solutions was 109.9 mEq/l, while that of birds on 37.5 per cent sea water was elevated to 134.8 mEq/l, sd 10.1.

TABLE 2

DISCRIMINATION BY WHITE-WINGED DOVES BETWEEN VARIOUS DRINKING SOLUTIONS

<i>Test solutions</i>	<i>Mean ml drunk/day</i>	<i>Length of test in days</i>	<i>Number of birds</i>	<i>t</i>	<i>P</i>
vs. Tap water	43.3				
12.5 per cent sea water	33.5	7	5	1.86	> .05
vs. Tap water	80.7				
25 per cent sea water	20.1	7	5	15.01	< .01
vs. Tap water	110.0				
37.5 per cent sea water	2.7	3	4	10.98	< .01
vs. 12.5 per cent sea water	61.1				
25 per cent sea water	23.5	7	5	11.06	< .01
vs. 25 per cent sea water	98.1				
37.5 per cent sea water	8.3	7	5	13.29	< .01
vs. 37.5 per cent sea water	59.0				
50 per cent sea water	11.6	7	4	6.41	< .01

Water deprivation.—The data for the effects of water deprivation on weight and survival are summarized in Figure 5 and Table 1. In both species weight loss was essentially linear, but the White-winged Doves lost weight less rapidly, tolerated greater losses in body weight, and survived longer.

Rehydration.—Rehydration experiments were carried out on 5 White-winged Doves and 10 Inca Doves which had been deprived of water for three and two days, respectively, and then placed back on *ad-libitum* tap water. These data are summarized in Table 1 and indicate that, when both species have lost approximately the same percentage of weight due

TABLE 3

DISCRIMINATION BY INCA DOVES BETWEEN VARIOUS DRINKING SOLUTIONS

<i>Test solutions</i>	<i>Mean ml drunk/day</i>	<i>Length of test in days</i>	<i>Number of birds</i>	<i>t</i>	<i>P</i>
vs. Tap water	15.5				
12.5 per cent sea water	13.9	7	5	1.14	> .05
vs. Tap water	17.4				
25 per cent sea water	11.5	7	10	2.45	< .05, > .01
vs. Tap water	17.4				
37.5 per cent sea water	6.1	7	5	10.14	< .01
vs. 12.5 per cent sea water	19.2				
25 per cent sea water	8.6	7	5	7.44	< .01
vs. 25 per cent sea water	34.1				
37.5 per cent sea water	4.1	7	5	12.37	< .01

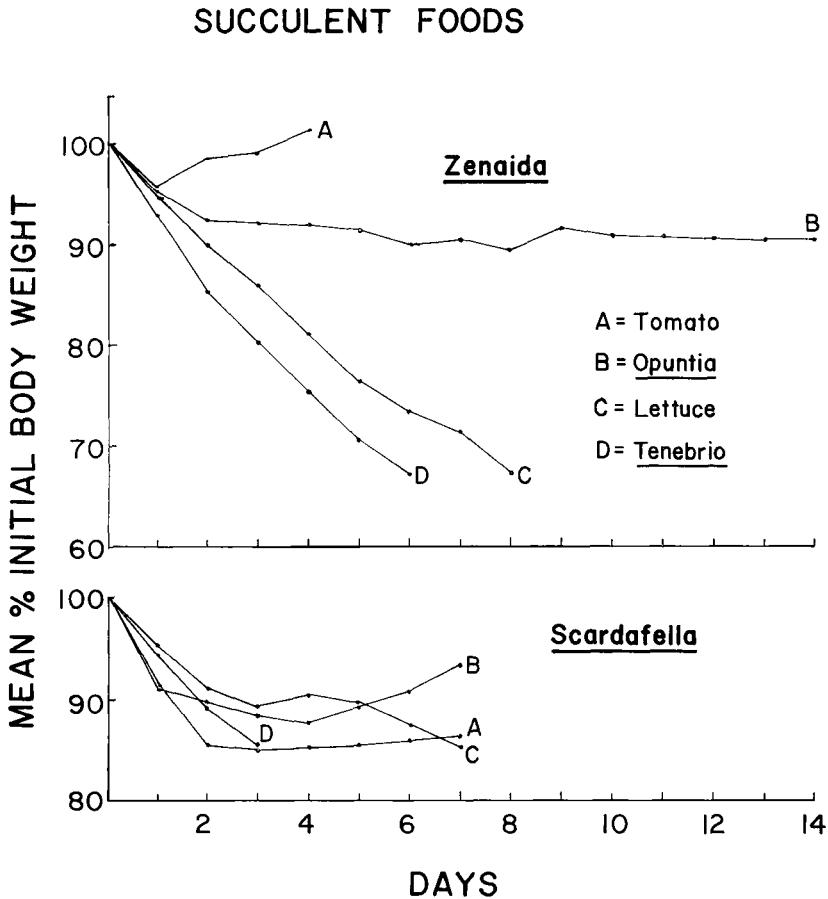


Figure 6. Changes in body weight of White-winged and Inca doves when provided with various succulent foods as water sources. The succulent foods employed were (A) halved tomatoes (95 per cent water by weight), (B) *Opuntia* fruit (85 per cent water), (C) chopped lettuce (95 per cent water), and (D) *Tenebrio* larvae, not eaten (62 per cent water).

to water deprivation, White-winged Doves are more effective in rehydration than are Inca Doves; the former are capable of drinking more water relative to their weight during the first five-minute period and gain more weight during the first hour than do the latter. During the first five minutes after water was restored, White-winged Doves drank 145 per cent of their mean *ad-libitum* daily consumption when normally hydrated, and 429 per cent of the mean daily minimal requirements; Inca Doves during the first five minutes drank only 118 and 146 per cent of their mean *ad-libitum* and minimal water intakes, respectively.

TABLE 4

RELATION BETWEEN BODY WEIGHT, SALINITY TOLERANCE, MINIMAL WATER REQUIREMENT, AND WATER DEPRIVATION IN THREE DOVES¹

Measurement	Species		
	Zenaida asiatica	Zenaidura macroura	Scardafella inca
Mean body wt., g	140.3	104.6	41.0
Maximum sea water percentage with wt. maintenance	37.5	25.0	25.0
Minimal tap or distilled water requirement, per cent body wt./day	4.2	2.8	8.5
Water deprivation, per cent body wt. lost/day	4.0	4.8	6.1

¹ Data for *Zenaidura macroura* from Bartholomew and MacMillen (1960) and MacMillen (1962).

Salinity discrimination.—Both species were highly discriminatory in their choice between drinking solutions of differing salinities (Tables 2 and 3). Neither showed preferences between tap water and 12.5 per cent sea water, but in all other combinations both invariably chose the least concentrated drinking solution.

Utilization of succulent foods as a water source.—It is clear that both White-winged and Inca doves can maintain weight and presumably positive water balance on at least some forms of succulent foods, together with mixed bird seed (Figure 6). Although the weight responses were somewhat different, both species maintained or gained weight, after an initial short period of weight loss, on fresh, halved tomatoes and *Opuntia* fruit (95 and 85 per cent water by weight, respectively). Both species ate fresh chopped lettuce (95 per cent water by weight), but White-winged Doves lost weight continuously while Inca Doves lost weight initially, gained slightly, and then continued to lose. Neither dove ate meal worms (*Tenebrio* larvae) (62 per cent water by weight) and they therefore lost weight steadily when these were provided.

DISCUSSION

Neither White-winged Doves nor Inca Doves show particularly striking adaptations in their water economies in spite of their general distribution in areas of desert. The major features of their water relations seem to conform most closely to the restrictions imposed upon them by body size. The only other North American desert dove for which comparative data are available (Bartholomew and MacMillen, 1960; MacMillen, 1962) is the Mourning Dove (*Zenaidura macroura*) which is intermediate in body size and generally intermediate in its water economy between White-winged Doves and Inca Doves (Table 4). The data for all three doves substantiate rather nicely the observed inverse relationship in birds between body size, evaporative water loss, and water intake, as well as the

probable inverse relationship between body size and weight loss during water deprivation (Bartholomew and Cade, 1963: 531). In addition, at least among these doves, there appears to be a direct relationship between body size and tolerance of saline drinking solutions, even though certain small land birds appear to be much more tolerant of concentrated saline water than many larger land birds (Bartholomew and Cade, 1963: 533).

Since the plasma osmotic pressure and chloride levels of White-winged Doves and Inca Doves appear to be very similar, and since White-winged Doves can utilize 37.5 per cent sea water while Inca Doves cannot exceed 25 per cent sea water, it may be presumed that these differences in salinity tolerance are due to differences in salt excretion. Scothorne (1959: 201) stated that salt-loaded homing pigeons (*Columba livia*) showed no indication of nasal gland secretion and we found no evidence of extra-renal salt excretion in White-winged and Inca doves, thus the kidney is indicated as the organ of salt excretion. Poulson (1965) has demonstrated a direct relationship between the urine-concentrating capacity and the number of Henle's loops in the avian kidney, and Marshall (1934: 148) and Benoit (1950: 342) stated that there is a direct relationship between the number of glomeruli (or nephrons) and body size for a variety of birds ranging from small passerines to domestic geese. Therefore we think that, exclusive of evaporative water loss, the differences in water relations (Table 4) between Inca Doves, Mourning Doves, and White-winged Doves are more closely related to body size, and hence differences in the abundance of nephrons and Henle's loops, than they are to any mechanisms specifically adapted in response to the different degrees of aridity and of water salinity with which these species must cope. Thus body size dictates urine-concentrating capacity of the bird and hence its salinity tolerances. If the larger White-winged Doves were better adapted specifically to aridity we would expect to find them under more rigorous desert conditions than the smaller Mourning Doves, which is contrary to our observations.

By virtue of more efficient kidneys and presumably lower rates of evaporative water loss White-winged Doves are more conservative in every respect in their water economy than are Inca Doves, and are thereby provided with equipment better able to cope with a strictly desert environment. Although when offered a choice of saline drinking solutions both species chose the least concentrated, the taste mechanism in White-winged Doves was not geared to maximal salinity tolerances. This incapacity of White-winged Doves to drink sufficient amounts of the tolerable 25 and 37.5 per cent sea-water solutions unless forced to drink by prior dehydration appears to be due to a salt repugnance, and suggests further that maximal kidney capacity is not directly related to processing saline solutions.

Both species appear to be opportunistic in their utilization of succulent foods as a water source (see Figure 6). In the laboratory and presumably in the field both doves are capable of maintaining or gaining weight while eating moist fruit (prickly pear and tomatoes; 85 and 95 per cent water, respectively) as the sole water source. The performance of the doves on chopped lettuce as a water source (95 per cent water) was rather variable even though it was readily eaten by both: White-winged Doves lost weight rapidly, while Inca Doves appeared to be nearly capable of at least temporary weight maintenance on that food. This capacity in Inca Doves may be related to the nearly constant presence of succulent grass in the lawns upon which they spend much of their time. Neither dove ate meal worms (62 per cent water) suggesting that insects are not important either in terms of diet or water economy.

While succulent fruit probably does not play a prominent role in the biology of the Inca Dove, we think that it may be very important, at least in Arizona, to White-winged Doves. Gilman (1911) reported that the spring arrival of White-winged Doves in south-central Arizona is coincident with the ripening of berries of the wild jujube, *Zizyphus (Condalia) lycioides*, upon which they "greedily" feed. Near Tucson, L. W. Walker (pers. comm.) tells us that White-winged Doves seem very dependent on saguaro cactus appearing in the spring when the first buds appear, and leaving in the fall when the last fruits fall to the ground. While White-winged Doves occur seasonally in parts of California and Mexico which lack saguaro cactus, in Arizona the distributions of White-winged Doves and saguaro appear to coincide, suggesting an interrelationship. In July, 1965, near Tucson we observed many White-winged Doves feeding on the moist, pulpy matrix of the central mass of newly opened, ripe saguaro fruit; these doves and many others had red-stained faces and throats denoting extensive use of the fruit. While it is very likely that the doves also find considerable nutrient value in the seeds contained in the central mass, our field and laboratory observations lead us to think that saguaro fruit (85 per cent water by weight) plays an important role in their water economy. Although White-winged Doves customarily fly considerable distances to water holes, they can maintain weight under unstressful laboratory conditions on prickly-pear fruit having the same water content as saguaro fruit. Similarly we think that during the saguaro fruiting season (July and August) White-winged Doves very likely could obtain sufficient water for maintaining positive water balance, even during high ambient temperatures, from newly opened saguaro fruit. This further suggests a symbiotic relationship, with the doves obtaining needed water and nutrients from saguaro fruit, and, in turn, dispersing saguaro seeds which may temporarily cling to the feathers or pass through the

feces. Alcorn *et al.* (1961) demonstrated that White-winged Doves were effective cross-pollinators of the self-sterile saguaro flowers by feeding on nectar, rich both in nutrients and water.

Like Mourning Doves (see MacMillen, 1962) both White-winged and Inca doves appear capable of rapid drinking and rehydration (Table 1), and very likely can make up routine water deficits in a very short time. Under natural circumstances, but where there is a plentiful supply of water in the form of lawn sprinklers and dripping faucets, Inca Doves appeared to be dainty drinkers and to satisfy their needs by frequent drinking in short, single draughts. White-winged Doves, which are more periodic in their drinking and probably use water holes only twice a day like Mourning Doves (Schmid, 1965), are greedy drinkers. On the evening of 7 July 1965 we observed numerous White-winged Doves drinking from an artificial, concrete-lined water hole in Saguaro National Monument, 20 miles west of Tucson. While drinking, and often standing in the water, the doves immersed their entire beaks, frequently to eye level, in the water and swallowed without cessation for about 8 sec. After satisfying their thirsts, the White-winged Doves immediately took flight and departed. The data in Table 1 also demonstrate the differences in drinking behavior between White-winged and Inca doves, and suggest that the former are more efficient in rehydration than are the latter.

The rather sedentary Inca Doves appear to be very closely tied, through their physiology and behavior, to a ready supply of water which is constantly available in their urban environment. However, they are only rarely seen outside of towns and villages which leads one to wonder about their native habitat prior to urbanization. Their dispersal from Mexico into the southwestern United States has been relatively recent and seems to have coincided with urbanization. Phillips *et al.* (1964: 43-44) state that none of the early explorers found this dove in Arizona, and that the first record of the Inca Dove was in 1872 at Fort Lowell, near Tucson, after which they became progressively more common. Similarly, the first record of an Inca Dove in Austin, Texas, was in 1889 after which time they soon became common throughout much of southern Texas (Bent, 1932: 444). In light of their high water requirements, the most likely native habitat for Inca Doves within the desert would have been river valleys with permanent water. Our search for them along the Sonoita River in southernmost Arizona was fruitless, although Mourning Doves, White-winged Doves, and Ground Doves (*Columbigallina passerina*) were all observed. However, Johnston (1960: 7) reports that a resident breeding population of Inca Doves occurs along the Río Cuchujaqui in southern Sonora, Mexico.

Thus both White-winged Doves and Inca Doves seem to conform in

water economy and distribution to limitations imposed upon them by body size and mobility. The larger, highly mobile White-winged Doves range freely throughout the desert and are able to meet their lower water demands with a greater variety of water sources. Conversely, the smaller, less mobile Inca Doves are confined to desert towns and villages where they can readily meet their more rigid water requirements with an abundance of fresh water.

ACKNOWLEDGMENTS

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SUMMARY

In the summer in southern Arizona strong-flying White-winged Doves are ubiquitous desert inhabitants while relatively sedentary Inca Doves are confined to towns and villages. White-winged Doves (140 g) are much larger than Inca Doves (41 g), and in southern Arizona are only summer residents while Inca Doves are resident throughout the year. These differences in body size, habitat preference, and mobility suggest related differences in water economy.

Laboratory studies indicate that White-winged Doves have lower *ad-libitum* and minimal water requirements, are more resistant to water deprivation and more effective in rehydration, and can maintain weight on more concentrated salt solutions than Inca Doves (37.5 and 25 per cent sea water, respectively). Both doves maintain fairly constant plasma osmotic pressure and chloride levels while drinking tolerable saline solutions. Both freely utilize succulent fruit as a water source in the laboratory, and field observations suggest that saguaro cactus fruit may play an important role in the water economy of White-winged Doves.

Field and laboratory data indicate that the smaller Inca Doves are restricted to desert towns because of their less versatile water requirements and less mobility, while the larger and highly mobile White-winged Doves range freely to meet their lower water demands with a greater variety of water sources.

LITERATURE CITED

- ALCORN, S. M., S. E. MCGREGOR, AND G. OLIN. 1961. Pollination of saguaro cactus by doves, nectar-feeding bats, and honey bees. *Science*, **133**: 1594-1595.
- BARTHOLOMEW, G. A., AND T. J. CADE. 1963. The water economy of land birds. *Auk*, **80**: 504-539.
- BARTHOLOMEW, G. A., AND R. E. MACMILLEN. 1960. The water requirements of Mourning Doves and their use of sea water and NaCl solutions. *Physiol. Zoöl.*, **33**: 171-178.
- BENOIT, J. 1950. Organes uro-génitaux. Pp. 341-377 in *Traité de zoologie*, tome XV (oiseaux) (P. P. Grassé, ed.). Paris, Masson and Co.
- BENT, A. C. 1932. Life histories of North American gallinaceous birds. U. S. Natl. Mus., Bull. 162.
- GILMAN, M. F. 1911. Doves on the Pima reservation. *Condor*, **13**: 51-56.
- JOHNSTON, R. F. 1960. Behavior of the Inca Dove. *Condor*, **62**: 7-24.
- MACMILLEN, R. E. 1962. The minimal water requirements of Mourning Doves. *Condor*, **64**: 165-166.
- MARSHALL, E. K., JR. 1934. The comparative physiology of the kidney in relation to theories of renal secretion. *Physiol. Rev.*, **14**: 133-159.
- POULSON, T. L. 1965. Countercurrent multipliers in avian kidneys. *Science*, **148**: 389-391.
- PHILLIPS, A. R., J. T. MARSHALL, JR., AND G. MONSON. 1964. *The birds of Arizona*. Tucson, Univ. Arizona Press.
- RIDGWAY, R. 1916. *The birds of North and Middle America*. U. S. Natl. Mus., Bull. 50 (pt. 7).
- SCHMID, W. D. 1965. Energy intake of the Mourning Dove, *Zenaidura macroura marginella*. *Science*, **150**: 1171-1172.
- SCOTHORNE, R. J. 1959. On the response of the duck and the pigeon to intravenous hypertonic saline solutions. *Quart. J. Exp. Physiol.*, **44**: 200-207.

Department of Zoology, Pomona College, Claremont, California. (Present address of second author: Department of Zoology, University of California, Los Angeles, California.)