WATER FLUX AND WATER REQUIREMENT IN FREE-LIVING ANTELOPE GROUND SQUIRRELS AMMOSPERMOPHILUS LEUCURUS

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Seasonal changes in H2O flux rates (H2O) were determined in free-living antelope ground squirrels (Ammospermophilus leucurus) in the Mojave Desert. Itemized H2O budgets were obtained for ground squirrels in the laboratory eating natural vegetation, seeds, and arthropods. Ground squirrels obtained excess H2O while eating succulent annual plants in the spring and arthropods. When provided with seeds and minimum H2O they decreased their evaporative H2O loss and reduced urinary and fecal H2O content. Changes in feeding rate, assimilation efficiency, or metabolic rate were unimportant in reducing H2O loss. In the field, H2O influx decreased from 238 ml kg−1 day−1 in the early spring to 85 ml kg−1 day−1 in the late fall and winter. This decrease paralleled a decrease in the H2O contents of the plants the ground squirrels consumed. The minimum H2O requirement of free-living ground squirrels was expressed as required minimum food H2O content. Leaves must be > 45% H2O to supplement an otherwise dry diet for A. leucurus. Other desert herbivores also generally require plant H2O contents of at least 40% for maintenance of H2O balance. However, plant H2O contents in the Mojave Desert drop below this level during the fall or winter of most years, at which time A. leucurus is most water stressed. Prior to winter rains, the inclusion of arthropods in the ground squirrel’s diet plays an essential role in its H2O balance.

INTRODUCTION

Adequate dietary water intake is essential to the survival of antelope ground squirrels (Ammospermophilus leucurus). These diurnal rodents inhabit arid regions of southwestern North America. Though laboratory studies have demonstrated they need some source of preformed water (Bartholomew and Hudson 1959; Hudson 1962; Maxson and Morton 1974), most wild ground squirrels have no access to free-standing water during most of the year. They are omnivores (Bradley 1968; Karasov 1982) and achieve water balance through consumption of arthropods or green vegetation. How much of these materials are necessary for water balance depends on many factors, including the food water contents, the fecal and urinary water loss associated with food consumption, and other aspects of the water budget such as evaporative water loss and metabolic water production. This study deals with this relationship between diet and water requirement in free-living antelope ground squirrels. Along with an earlier study (Karasov 1982), its overall goal is to determine the extent to which specific nutritional requirements, and the suitability of various dietary items in meeting those requirements, play a role in the diet of these omnivorous mammals.

This paper adds to knowledge from earlier studies (Hudson 1962; Maxson and Morton 1974) by relating the water requirement of A. leucurus more directly to diet and by presenting the first data on the water relations of a wild population. Water budgets were constructed for ground squirrels eating various foods in
the laboratory, and a general model was derived for determining the required water content and amount of a dietary water supplement necessary for omnivores or herbivores to achieve water balance. Water influx and efflux were measured with tritiated water ($^{3}$H$_{2}$O) in free-living and caged antelope ground squirrels in the field to compare with laboratory measurements (Yousef et al. 1974) and to determine A. leucurus's seasonal water balance status.

METHODS

FIELD STUDIES

Field studies were performed in 1977 and 1978 at the Barstow Unified School District's Desert Research Station about 20 km northwest of Barstow, San Bernardino County, California, in the Mojave Desert. Perennial vegetation on the site was primarily Atriplex spp. and Lycium pallidum. Annual rainfall averages about 10 cm in this area, but yearly totals have been as low as 3 cm and as high as 27 cm (station records). Precipitation from May 1977 to April 1978 was 27 cm.

Two methods were used to evaluate the degree of water stress to which free-living Ammospermophilus leucurus were subjected. Water flux in free-living ground squirrels was measured and compared with that of captive, water-restricted ground squirrels. Also, urine osmotic pressure of field-collected ground squirrels was compared with the maximum urine osmotic pressure of ground squirrels on minimum $^{3}$H$_{2}$O in the laboratory.

Water flux in free-living antelope ground squirrels was measured on ten occasions between May 1977 and December 1978 with tritiated water ($^{3}$H$_{2}$O). Trapping, injection, and sampling methods are described in Karasov (1981). Ammospermophilus leucurus were live trapped and injected with 0.5–1.0 ml of $^{3}$H$_{2}$O containing 0.1 mCi $^{3}$H/ml. After 3 h a 0.15 ml blood sample was taken from the infraorbital sinus and each animal was weighed and then released. No lactating females were used. Animals were re-captured after 5–7 days and were re-weighed, and a second blood sample was taken. Blood samples were distilled, and the $^{3}$H$_{2}$O was analyzed for $^{3}$H activity by liquid scintillation spectrometry. Total body $^{3}$H$_{2}$O was determined by drying some animals and by the dilution technique (Foy and Schnieden 1960). (Tritium dilution overestimated body $^{3}$H$_{2}$O by about 5% [personal observation; Nagy and Costa 1980], so calculations were adjusted accordingly.) Water efflux and influx were calculated using equations 4 and 6 of Nagy and Costa (1980).

Water flux in captive, $^{3}$H$_{2}$O-restricted A. leucurus was measured under seminatural conditions at the study site in August and October 1978. Ground squirrels were conditioned by maintaining them on ad lib. crimped oats with small amounts of carrot provided every few days. After this preparatory stage they were labeled with $^{3}$H$_{2}$O and placed alone in small outdoor enclosures (1 m diameter) constructed of 0.635-cm hardware cloth (walls and ceiling). Each enclosure had an artificial burrow made of 0.635-cm hardware cloth which was wrapped with fine screen and which extended to a depth of 60–70 cm in the soil. Animals were given various amounts of carrot daily during the 3–5-day measurement period and were then removed, weighed, and sampled.

Urine samples were collected from freshly captured wild animals during handling or over mineral oil at various times during the field study. These were stored in 75-μl heat-sealed glass capillary tubes, frozen immediately, and analyzed later at the University of California, Los Angeles, with a Wescor 510B Vapor Pressure Osmometer. When urine concentrations exceeded the capacity of the osmometer they were diluted 1:2 with distilled water and measured again.

Average environmental conditions at the study site were taken from National Weather Service records for Barstow, California (20 km away), and measurements made at the study site with a WeatherMeasure Model H311 Hygrothermograph placed on the ground in the shade. Average maximum and minimum relative humidities for several months of the year were calculated from 8–12 days of hygrothermograph data from each month. Temperatures in the artificial burrows were measured with a Yellow Springs Instruments thermistor ther-
mometer, and relative humidity was recorded with a Thunder Scientific Hygrometer (Model HSP-100).

LABORATORY STUDIES

Goals of the laboratory feeding studies were to (1) test the accuracy of isotope measurement of H₂O influx, (2) construct a minimum H₂O loss budget which would serve as a starting point for subsequent analyses, and (3) determine the effectiveness of arthropods and moist spring plant material as water sources.

The accuracy of isotope measurement of net H₂O flux was determined by comparing H₂O influx measured gravimetrically with the isotopic measurement. Over a period of 10 wk, five H²H₂O labeled A. leucurus received ad lib. laboratory chow (Wayne Lab Blox; 6% H₂O) plus ad lib. H₂O, one-half ad lib. H₂O, and then one-third ad lib. H₂O. At this point their body masses were 90% of initial. At each watering level, H₂O consumption was measured by weighing H₂O bottles and correcting for both evaporation and spillage. Metabolic H₂O production was estimated from metabolic rates determined by energy assimilation (kJfood − kJfeces; Phillipson microbomb calorimeter) and a conversion factor of 0.029 ml H₂O (kJ metabolized)^⁻¹ (Schmidt-Nielsen 1975). Total H₂O influx from isotope turnover was calculated as described above.

Twelve A. leucurus captured near the study site were used in feeding trials to quantify the routes of H₂O loss. They were labeled with H²H₂O, placed in metabolic cages (Econo-Metabolism units, Maryland Plastics), and fed one of three diets: (1) whole adult crickets ad lib., (2) freshly collected fruiting parts of the two most important annual plants in the spring diet (Karaszov 1982)—Erodium cicutarium (66% of experimental diet by dry mass) and Gilia latiflora (34%) ad lib., and (3) crimped oats ad lib. plus carrot.

The arthropod and plant feeding trials lasted 5 days after an initial 4-day adjustment period. No drinking water was provided in any of the trials. The amount of carrot provided to the animals eating crimped oats was decreased over a period of 4 wk during which time the animals' body masses decreased 15%. At this point they were provided with ad lib. oats but just enough carrot to maintain constant body mass.

Food intake was measured by the difference between what was given and what remained each day, after correction for water content. The funnel design of the cages allowed separate collection of urine and feces. At the end of the experiment the chamber floors and funnels were washed with hot distilled water to collect any remaining urine. Fresh feces and urine samples were collected periodically at night and day (lights on 0700–1900 hours) during handling and by placing ground squirrels in small hardware cloth cages over mineral oil for 6 h. Food, fecal, and urine H₂O contents were determined by drying fresh samples to constant mass at 70 C.

Water influx in these experiments was not directly measured because the ground squirrels did not eat the food presented to them immediately. Because of evaporation, the H₂O content of each food at the time of consumption was less than when the foods were presented. (When foods were first placed in the metabolic cages they had the following H₂O contents: crickets, 1.8 ml [g dry mass]^⁻¹; plant fruiting parts, 2.5 ml [g dry mass]^⁻¹; carrots, 6.0 ml [g dry mass]^⁻¹.)

Evaporative H₂O loss of animals in the laboratory was determined in two ways. One estimate was to subtract fecal and urine H₂O loss from total efflux measured with H²H₂O. Evaporative H₂O loss rates of animals provided with ad lib. oats and limited amounts of carrot were also determined by measuring rates of mass change during the last 12 h of a 36-h fast. (In a fasting mammal [RQ (respiratory quotient) ~ 0.7] mass change due to respiratory loss of CO₂ is approximately balanced by a greater retention of O₂ which is incorporated into metabolic H₂O. Thus, any mass decrease is largely due to evaporation or urinary and fecal loss.) The animals were placed for 12 h (1000–2200 hours) over tared containers with mineral oil for collection and weighing of any urine or feces excreted.

Numerical results are given as mean ± standard deviation (no. = number of animals in the sample). The t-test (P < .05) was used for tests of difference between
means and for significance of linear regression.

RESULTS

VALIDATION

Water influx was accurately measured by H\textsuperscript{3}HO turnover in antelope ground squirrels in the laboratory. In 13 paired comparisons of gravimetrically measured influx and isotopically measured influx, there was no significant difference between the two measures ($t = 0.27, P > .5$, paired $t$-test). The average difference (defined as $100 \times [\text{H}^3\text{HO value} - \text{gravimetric value}] / \text{gravimetric value}$) was $+0.1 \pm 9.3\%$ for animals whose total influx ranged 65–165 ml kg$^{-1}$ day$^{-1}$. Since influx rates are mathematically derived from efflux rates, H\textsuperscript{3}HO must also accurately measure H\textsubscript{2}O efflux in Ammospermophilus leucurus under these conditions. This is important since I estimated evaporative H\textsubscript{2}O loss by subtraction from total H\textsubscript{2}O efflux. Interestingly, there was no detectable overestimate due to H\textsubscript{2}O vapor influx. Nagy and Costa (1980) found that entry of H\textsubscript{2}O through lungs and skin by condensation from ambient vapor resulted in a 6–10-ml kg$^{-1}$ day$^{-1}$ overestimate in H\textsubscript{2}O influx in labeled kangaroo rats at the same absolute humidity.

EFFECTS OF DIET AND H\textsubscript{2}O RESTRICTION ON H\textsubscript{2}O LOSS

Ground squirrels eating fresh plant parts and crickets obtained excess H\textsubscript{2}O as evidenced by their higher fecal and urinary H\textsubscript{2}O contents and higher evaporative H\textsubscript{2}O loss rates compared with H\textsubscript{2}O-restricted ground squirrels (table 1). Fecal H\textsubscript{2}O contents were twice as high in the ground squirrels fed succulent foods and, in general, were correlated ($P < .001$) with total H\textsubscript{2}O influx (fig. 1). Fecal H\textsubscript{2}O loss was highest in the plant eaters in part because the plant eaters produced more feces when eating the less digestible plant material. The evaporative H\textsubscript{2}O loss rate of plant and cricket eaters, about 7% of body mass per day, was about twice that of the H\textsubscript{2}O-restricted group. Evaporative H\textsubscript{2}O loss measured by the rate of mass change in the H\textsubscript{2}O-restricted group ($36.9 \pm 11.6$ ml kg$^{-1}$ day$^{-1}$) was not significantly different from the tritium estimate in the same animals (table 1, $t = 1.19, P > .2$, paired

<table>
<thead>
<tr>
<th>TABLE 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>DRY MASS FLUX AND WATER EFFLUX IN LABORATORY “AMMOSPERMOPHILUS LEUCURUS” FED THREE DIETS WITHOUT DRINKING WATER</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Diet and Avenue</th>
<th>Body Mass of Experimental Animals (g)</th>
<th>Dry Mass Flux (g kg$^{-1}$ day$^{-1}$)</th>
<th>Water Content (ml/g dry mass)</th>
<th>Water Efflux (ml kg$^{-1}$ day$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crickets (no. = 4): Food</td>
<td>88.1</td>
<td>74.3 (10.5)</td>
<td>14.8 (6.8)</td>
<td>161.3 (18.2)</td>
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<td></td>
<td>Feces</td>
<td>10.9 (2.6)</td>
<td>7.17 (7.2)</td>
<td>71.0 (8.4)</td>
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<td></td>
<td>Urine</td>
<td>10.7 (2.2)</td>
<td>7.17 (7.2)</td>
<td>71.0 (8.4)</td>
</tr>
<tr>
<td></td>
<td>Evaporation*</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
</tr>
<tr>
<td>Plant parts (no. = 3): Food</td>
<td>78.0</td>
<td>98.1 (9.1)</td>
<td>56.0 (13.9)</td>
<td>173.0 (17.0)</td>
</tr>
<tr>
<td></td>
<td>Feces</td>
<td>31.3 (8.7)</td>
<td>10.10 (1.7)</td>
<td>42.0 (15.4)</td>
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<tr>
<td></td>
<td>Urine</td>
<td>4.0 (.9)</td>
<td>10.10 (1.7)</td>
<td>42.0 (15.4)</td>
</tr>
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<td></td>
<td>Evaporation*</td>
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<td>. . .</td>
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<tr>
<td></td>
<td>Total</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
</tr>
<tr>
<td>Oats + minimum carrot (no. = 5): Food</td>
<td>73.0</td>
<td>53.5 (7.3)</td>
<td>3.2 (.8)</td>
<td>48.6 (7.1)</td>
</tr>
<tr>
<td></td>
<td>Feces</td>
<td>4.2 (.9)</td>
<td>.76 (.14)</td>
<td>3.2 (.8)</td>
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<tr>
<td></td>
<td>Urine</td>
<td>3.3 (.4)</td>
<td>4.05 (.47)</td>
<td>13.6 (2.9)</td>
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<tr>
<td></td>
<td>Evaporation*</td>
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<td>. . .</td>
<td>. . .</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>. . .</td>
<td>. . .</td>
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</table>

Note.—Results given as means with SDs in parentheses.
* Evaporation obtained by difference. Total efflux measured with H\textsubscript{3}HO.
Urinary osmotic pressures of the cricket eaters varied with time of collection (0900-1800 hours, 1,455 ± 189 mosmol kg⁻¹, no. = 4; 2000-0800 hours, 2,636 ± 196, no. = 4) but were lower than those of the H₂O-restricted group (3,100 ± 212, no. = 6) which did not vary with time of collection. In the field, mean urine osmotic pressure of freshly captured ground squirrels was inversely related to mean H₂O influx (fig. 2). Mean urine osmotic pressure of the December group, 2,718 ± 525 mosmol kg⁻¹ (no. = 12), was not significantly different from the mean urine osmotic pressure of H₂O-restricted laboratory animals (t = 1.54, P > .1). (Samples from freshly captured animals may not represent the actual average urine concentrations of wild animals because of possible stress-induced diuresis [Carpenter 1966] or diurnal variation in mean urine osmotic pressure. However, the general pattern occurring in the wild should still be reflected in these values.) Overall, the ground squirrels responded to H₂O restriction by reducing H₂O efflux through every avenue of H₂O loss.

Other ways by which mammals might minimize H₂O loss during H₂O restriction include (1) increased assimilation efficiency and decreased food intake, which result in less H₂O loss via urine and feces; and (2) decreased metabolism (respiration), which can reduce evaporative H₂O loss. The data for *A. leucurus* indicate that these adaptations are not important in its overall response to H₂O restriction. First, H₂O restriction had only a minor effect on feeding rates of *A. leucurus* (table 2). Second, H₂O restriction had no significant effect on assimilation efficiency (table 2). Third, since the ground squirrels maintained constant body masses in these H₂O restriction experiments on chow or seed diets, and their feeding rates were similar, it follows that their metabolic rates were likewise similar.

**FIELD STUDIES**

Measurements on animals in outdoor enclosures suggested that the minimum H₂O requirement under natural conditions may be higher than in the laboratory. The environmental conditions encountered by ground squirrels in outdoor enclosures were different from conditions in the laboratory and depended on whether ground squirrels were in burrows or the open air (fig. 3). The mean total H₂O efflux of the H₂O-restricted ground squirrels in enclosures was 67 ± 5 ml kg⁻¹ day⁻¹ (no. = 10
Fig. 3.—Average temperature and humidity during four periods at the study site and in the laboratory. Shown are ambient air maxima and minima (solid lines) and average values in the artificial burrows (broken lines). Laboratory values are maxima and minima.

observations on 6 animals), 39% higher than the total efflux of the H₂O-restricted ground squirrels in the laboratory eating the same food (table 1). Water influx of the ground squirrels in enclosures varied because each received a different amount of carrot daily. Body mass was significantly correlated with H₂O influx (fig. 4), and this relationship predicts that a ground squirrel could maintain body mass when its H₂O influx rate was 68 ml kg⁻¹ day⁻¹. If it is assumed that fecal and urinary H₂O loss was similar in the laboratory and field enclosures (metabolic rates and calculated feeding rates were similar [personal observation]), and that there was no major dif-

Fig. 4.—Body mass change rate (100 × ln [massfinal/massinitial]/time) vs. H₂O influx in antelope ground squirrels offered crimped oats ad lib. and restricted amounts of carrot while maintained in outdoor enclosures. The least-squares regression equation is y = −6.31 + 0.923x, r² = .75 (P < .005).

### TABLE 2

<table>
<thead>
<tr>
<th>Diet and Regime</th>
<th>Body Mass of Experimental Animals (g)</th>
<th>Water Influx (ml kg⁻¹ day⁻¹)</th>
<th>Dry Matter Intake (g kg⁻¹ day⁻¹)</th>
<th>D* (%)</th>
</tr>
</thead>
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<tr>
<td>Laboratory chow:</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>+ ad lib. H₂O</td>
<td>80.9</td>
<td>142.9</td>
<td>110.3</td>
<td>67.4</td>
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<tr>
<td>(no. = 5)</td>
<td>(18.1)</td>
<td>(13.8)</td>
<td>(4.1)</td>
<td>(3.4)</td>
</tr>
<tr>
<td>+ ½ ad lib. H₂O</td>
<td>70.4</td>
<td>67.3</td>
<td>37.2</td>
<td>62.1</td>
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<tr>
<td>(no. = 4)</td>
<td>(4.3)</td>
<td>(3.7)</td>
<td>(3.7)</td>
<td>(1.6)</td>
</tr>
<tr>
<td>Oats:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>+ ad lib. H₂O</td>
<td>88.9</td>
<td>. . .</td>
<td>58.8</td>
<td>90.2</td>
</tr>
<tr>
<td>(no. = 3)</td>
<td>. . .</td>
<td>. . .</td>
<td>(3.0)</td>
<td>(4)</td>
</tr>
<tr>
<td>+ minimum carrot</td>
<td>73.0</td>
<td>48.6</td>
<td>. . .</td>
<td>53.5b</td>
</tr>
<tr>
<td>(no. = 5)</td>
<td>(7.1)</td>
<td>(7.3)</td>
<td>(1.3)</td>
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</tr>
</tbody>
</table>

**Note.**—Results are given as means with SDs in parentheses. For each diet, there was no significant difference in mean feeding rate or D between the two water regimens.

* D = dry matter assimilation = 100 × (gfood − gfruit)/gfood.
* Seeds only. The small amount of carrot consumed had an insignificant effect on calculated D.
ference in vapor influx, ground squirrels in enclosures had calculated (by subtraction) evaporative H₂O loss rates of 50 ml kg⁻¹ day⁻¹, about 50% higher than in the laboratory.

Water influx and efflux rates of free-living *A. leucurus* were not significantly different from each other during any measurement period, and field animals almost always maintained constant body masses. Influx rates were highest in the spring of each year and were also high in August 1977, after a heavy rain (fig. 5A). Without heavy summer rains, H₂O influx decreased through the year from 238 ± 18 ml kg⁻¹ day⁻¹ (no. = 4) in February 1978 to 85 ± 16 (no. = 5) in December 1978.

Antelope ground squirrels drank very little or not at all when free-standing H₂O was available, and changes in H₂O influx corresponded directly to changes in plant H₂O contents. Rain puddles were on the ground during two measurement periods: the second week of May 1977 and the third week of August 1977. Animals labeled with H³PO₄ during the period in which puddles were on the ground in August had H₂O influx rates one-half those of animals labeled 1 wk later when the puddles had dried (fig. 5C). The influx rates during the first period (121 ± 8 ml kg⁻¹ day⁻¹) were less than those of laboratory animals with ad lib. H₂O (table 2, t = 2.77, P < .025) but the same as those of free-living animals in August 1978 when there was no free-standing H₂O (128 ± 13). Water influx rates during the other period when free-standing H₂O was available (May) were also lower than influx rates measured 1–2 wk later when puddles were dry but

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**Fig. 5.—A.** Water contents of some plants consumed by antelope ground squirrels at the study site. New leaves grew on *Lycium pallidum*, the most important perennial plant in the diet, following rain late in August 1977. Most annual plants (*Gilia latiflora*, *Eremalche esilis*, *Erodium cicutarium*, and *Amsinckia tessellata*) were dry by summer but *Salsola iberica* remained hydrated longer. **B.** Weekly precipitation at Barstow, California, 20 km from the study site. **C.** Water influx rates of free-living antelope ground squirrels during periods when free-standing H₂O was (○) and was not (●) available. Points are means and vertical lines are 95% confidence intervals. Numbers in parentheses are the number of animals in the sample. Shown also are the minimum H₂O influx rates required for body mass maintenance of antelope ground squirrels when in the laboratory (dashed line) and when in outdoor enclosures (dotted line).
new vegetation had appeared. Increased 
H\textsubscript{2}O influx following rains was due to con-
sumption of new plant growth. In general, 
changes in H\textsubscript{2}O influx corresponded to 
changes in plant H\textsubscript{2}O content at the site 
and changes in diet. When succulent an-
uual plants were present early in the year 
(January–May), H\textsubscript{2}O influxes were high. 
The death of most annuals and the de-
hydration of perennial plants in the sum-
mer and the increased consumption of 
seeds in the fall (Karasov 1982) were par-
alleled by decreases in H\textsubscript{2}O influx in the 
ground squirrels (fig. 5A, C).

DISCUSSION
WATER REQUIREMENTS

A central element in understanding 
Ammospermophilus leucurus's feeding 
ecology is the determination of the 
minimum H\textsubscript{2}O content necessary for plant 
leaves to serve as an H\textsubscript{2}O supplement. (An 
H\textsubscript{2}O supplement is defined here as a 
source of preformed H\textsubscript{2}O which, when 
added to an otherwise too-dry diet, results 
in H\textsubscript{2}O balance.) Antelope ground squir-
rels can use relatively abundant plant ma-
terial to meet their H\textsubscript{2}O requirement as 
long as plants are not too dry. Plants usu-
ally progressively dry out after spring in 
the desert, and once they become too dry 
arthropods are the primary potential 
source of supplementary H\textsubscript{2}O. The ground 
squirrels might have to modify their foraging behavior to locate enough of this 
scarcer resource. A simple formula is used 
below to estimate the required minimum 
plant H\textsubscript{2}O content and the amount of 
arthropod required for H\textsubscript{2}O balance if plant 
H\textsubscript{2}O contents fall below this level.

Unless a gram of plant material contains 
more H\textsubscript{2}O than the amount lost via feces 
and urine in processing that gram, no mat-
ter how much plant is consumed a ground 
squirrel will still be in negative H\textsubscript{2}O bal-
ance when eating only that plant. For a 
ground squirrel consuming summer or fall 
plant matter with an assimilable electrolye 
and N content of about 2.5 mosmol (g 
dry mass\textsuperscript{-1}) (Nagy, Shoemaker, and Costa 
1976), a dry matter assimilability of 55% 
(Karasov 1982), and excreting maximally 
concentrated urine (3.5 mosmol (ml 
H\textsubscript{2}O\textsuperscript{-1}) (Hudson 1962; Maxson and Mor-
ton 1974; this study)) and maximally de-
hydrated feces (0.65 ml H\textsubscript{2}O [g dry 
mass\textsuperscript{-1}; fig. 1]), this processing loss of 
H\textsubscript{2}O, l, is 0.86 ml H\textsubscript{2}O (g dry mass 
food\textsuperscript{-1}). However, in actuality, whenever 
there are other food items in the diet which 
have H\textsubscript{2}O processing losses greater than 
their H\textsubscript{2}O contents, g\textsubscript{i}, or whenever 
evaporative H\textsubscript{2}O loss, m\textsubscript{e}, exceeds 
metabolic H\textsubscript{2}O production, m\textsubscript{m} (the case 
for A. leucurus at 25 C, 25%-50% RH), the 
minimum H\textsubscript{2}O content necessary to 
qualify as an H\textsubscript{2}O supplement is a more 
complex function of the total H\textsubscript{2}O budget 
and the proportion of the total metaboliz-
able energy intake supplied by the H\textsubscript{2}O 
supplement. A simple model (see Appen-
dix) which formalizes this relationship for 
a mixed diet is:

\[
g_s = l_s + \frac{c_s}{\rho} \sum q_i \frac{g_i}{c_i} (l_i - g_i) \\
+ \frac{c_s}{M \rho} (m_e - m_m),
\]

where the subscript s refers to the food 
which also represents an H\textsubscript{2}O supplement 
and satisfies the proportion \( \rho \) of the daily 
energy requirements (\( M \)), and the sub-
script i refers to other food types in the diet 
which satisfy the proportion \( q \) of the daily 
energy requirements. The letter c denotes 
the metabolizable energy content of a par-
ticular food. (See table A1 for definitions 
of symbols and their measured or 
estimated values.)

In the case of plant material providing 
the only H\textsubscript{2}O supplement to an otherwise 
dry diet (seeds perhaps), \( g_s \) is minimized as 
\( \rho \) approaches 1.0 and \( q \) approaches 0. In 
other words, for A. leucurus in such a 
situation, the minimum H\textsubscript{2}O content 
necessary for plant leaves to serve as an H\textsubscript{2}O 
supplement would be more than 0.86 ml (g 
dry mass\textsuperscript{-1}) and would vary according to 
the proportion of seeds and vegetation in 
the diet. Calculations similar to these but 
for a more digestible spring diet resulted in 
a required minimum plant H\textsubscript{2}O content of 
0.85 ml (g dry mass\textsuperscript{-1}).

How well can arthropods serve as an 
H\textsubscript{2}O supplement? In the laboratory feeding 
trial, if ground squirrels had excreted 
maximally concentrated urine and de-
hydrated feces, they would have lost about 
0.7 ml H\textsubscript{2}O per gram dry arthropod con-
assumed. Since the crickets contained 1.8 ml H₂O (g dry mass)⁻¹, they provide more than 1 ml H₂O (g dry mass)⁻¹ in “extra” H₂O which can go toward meeting requirements for evaporative H₂O loss and the excretion of feces and osmolites of any dry foods in a diet. In short, arthropods provide an excellent source of supplementary H₂O for A. leucurus. In the field, when free H₂O is unavailable, arthropods (or fresh vertebrate flesh) are the only source of supplementary H₂O when plant H₂O contents fall below about 0.9 ml (g dry mass)⁻¹.

Leaf H₂O contents fell below this level in 1978 (fig. 5) and every other year for which there are records at this site (Nagy et al. 1976). During the weeks just prior to winter rains there are no plants with adequate H₂O in this habitat. Free-living antelope ground squirrels do maintain H₂O balance at this time, and diet studies indicate they do so by increasing their consumption of arthropods (Bradley 1968; Karasov 1982). Equation (1) can be rearranged to calculate how much arthropod must be consumed for H₂O balance. Depending on the particular values used in the calculation (table A1), the prediction is that 20%–30% of the diet should be arthropod. Arthropods have been estimated to make up 36% (Bradley 1968) and 18% (Karasov 1982) of the diet of A. leucurus at two sites in the Mojave Desert during the month just prior to the winter rains. At both sites arthropod proportion of the diet decreased to 1%–2% in the month following winter rains when new plant growth appeared. These data suggest that A. leucurus modifies its winter diet in response to its need for H₂O. However, complete analysis of this possibility requires consideration of changes in arthropod abundance also (Karasov, in preparation).

COMPARATIVE H₂O RELATIONS OF FREE-LIVING DESERT ANIMALS

The H₂O influx rates and urine osmotic pressure of free-living A. leucurus indicate that ground squirrels were most H₂O stressed during December. Urine concentrations were highest then, and several freshly captured ground squirrels had urine osmotic pressures as high as 3,300 mosmol kg⁻¹, close to the maximum for A. leucurus. Water influx in December was lower than at any other time of the year and was near the predicted minimum required H₂O influx of H₂O-restricted ground squirrels in outdoor enclosures. (The minimum required H₂O influx of free-living ground squirrels eating a mixed diet may be even higher than that of ground squirrels in enclosures. This is because consumption of arthropods and plant material results in higher urinary and fecal H₂O loss [table A1].) Antelope ground squirrels in winter share burrows (Karasov 1983), and high humidity caused by grouped animals, or isotope recycling between grouped animals, could result in, respectively, an over- or underestimate of H₂O flux measured by H³PO turnover (Nagy and Costa 1980). However, the trends in H₂O influx during the rest of the year, and in urine osmotic pressure, leave little doubt that it is during the weeks just prior to winter rains that A. leucurus is most H₂O stressed.

In contrast, seasonal trends in H₂O influx and urine osmotic pressure in three nocturnal granivorous rodents seem reversed (MacMillen and Christopher 1975). Urine concentration in the granivores peaked in the summer–early fall and was lowest during the winter when there was a more favorable relationship between evaporative H₂O loss and metabolic H₂O production (MacMillen and Christopher 1975). Field H₂O flux in the granivores was highest during the winter and lowest during the summer. The herbivorous Lepus californicus was more similar to A. leucurus in that the weeks just prior to winter rains were the period least favorable with regard to its H₂O balance (Nagy et al. 1976).

Seasonal variation in H₂O flux in these desert mammals differs because of differences in diet, behavior, and varying abilities to reduce H₂O loss. The relation between evaporative H₂O loss and metabolic H₂O production has a much greater effect on total H₂O balance in granivorous species than herbivorous species because of the relatively low fecal and urinary H₂O loss of the former ani-
mals. These studies also demonstrate that analysis of H₂O flux in free-living animals cannot be on the basis of body mass alone, as has been done for laboratory animals (see Nicol 1978 and references therein). This is because wide variation in dietary H₂O intake can obscure variation associated with differences in body mass. For example, depending on season and diet, the H₂O influx (calculated from H²H₂O turnover) of A. leucurus (ml day⁻¹) can be the same or as much as seven times higher than the influx of a free-living kangaroo rat half its size (MacMillen and Christopher 1975), the same or 40% of the influx of a free-living woodrat 50% larger (Grenot and Serrano 1979), or 50% higher or lower than its own influx under standardized conditions in the laboratory (Yousef et al. 1974; table 2).

Few other desert herbivores can maintain constant body mass on plant diets with lower H₂O contents than A. leucurus (table 3). The minimum amount of H₂O lost in eliminating food residues and the evaporative H₂O loss rate determine the minimum required H₂O content. Neotoma lepida (Lee 1963; Stallone 1979) and L. californicus (Nagy et al. 1976) have higher ratios of evaporative H₂O loss:metabolic H₂O production than A. leucurus and use more H₂O in processing a gram of plant food (less concentrated urine) than does A. leucurus (table 3). Though Eleodes armata and Sauromalus obesus have lower absolute evaporative H₂O loss rates than any of the mammals, they have much less favorable relationships between metabolic H₂O production and evaporative H₂O loss (table 3). Eleodes armata has the lowest predicted required leaf H₂O content primarily because it loses so little H₂O in processing each gram of food consumed. It excretes feces with as little as 0.25 ml H₂O (g dry mass)⁻¹ (Cooper 1981). Another plant eater which may be able to maintain constant body mass on drier plants is Diplotomys micros in the Great Basin Desert (Kenagy 1973). This kangaroo rat shaves off the salty cuticle of Atriplex confertifolia leaves before eating them so its electrolyte input is greatly reduced.

Though most of the desert animals listed in table 3 require plants with at least 40% H₂O, plant H₂O contents in the Mojave Desert drop below this level during the fall or winter of most years (Nagy et al. 1976; fig. 5A). How do leaf-eating animals of the Mojave Desert survive when plants are too dry? Jackrabbits (Nagy et al. 1976) and woodrats (Lee 1963; Schmidt-Nielsen 1964) are probably restricted to certain areas with either succulent vegetation or free H₂O. Otherwise, they lose body mass and perhaps die during dry periods. Low mass-specific rates of metabolism and H₂O efflux in Sauromalus (Nagy 1972) and Eleodes (Cooper 1981)

### TABLE 3

<table>
<thead>
<tr>
<th>Animal</th>
<th>Body Mass (kg)</th>
<th>I (ml [g dry mass]⁻¹)</th>
<th>mₑ (ml kg⁻¹ day⁻¹)</th>
<th>mₑ (ml kg⁻¹ day⁻¹)</th>
<th>Eₑₑₑ (ml [g dry mass]⁻¹)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eleodes armata (darkling beetle)</td>
<td>.001</td>
<td>.12</td>
<td>19.1</td>
<td>2.4</td>
<td>.76</td>
<td>Cooper (1981)</td>
</tr>
<tr>
<td>Ammospermophilus leucurus</td>
<td>.10</td>
<td>.86</td>
<td>32</td>
<td>28</td>
<td>.9</td>
<td>This study</td>
</tr>
<tr>
<td>Neotoma lepida (desert woodrat)</td>
<td>.14</td>
<td>&gt;1.56</td>
<td>Lee (1963)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sauromalus obesus (chuckwalla)</td>
<td>.17</td>
<td>.97</td>
<td>12.3</td>
<td>3.4</td>
<td>1.67</td>
<td>Nagy (1972)</td>
</tr>
<tr>
<td>Lepus californicus (black-tailed jackrabbit)</td>
<td>1.8</td>
<td>1.1</td>
<td>25</td>
<td>15</td>
<td>1.4</td>
<td>Nagy et al. (1976)</td>
</tr>
</tbody>
</table>

Notes.—Symbols are defined in table A1.
result in low rates of body mass loss, so imbalance is not as critical as in endothermic animals. *Sauromalus* were inactive and did not eat during the late summer and the cool dry fall and winter months. Raising of food H2O content by storage in a moist burrow is important in the H2O balance of kangaroo rats (Schmidt-Nielsen 1975), and this might be of some adaptive value to leaf eaters.

Another alternative is to incorporate into the diet arthropods or fresh carrion, the only foodstuffs with adequate H2O during periods when plants are too dry. As discussed above, arthropods make an excellent H2O supplement for *A. leucurus*. Thus, a major conclusion of this study is that late in the year, H2O can represent an important nutrient constraint in the feeding ecology of *A. leucurus*. The inclusion of arthropods in the ground squirrel's diet should, and does, play an important role in its H2O balance maintenance during the fall and early winter.

**APPENDIX**

**CALCULATION OF MINIMUM H2O CONTENT FOR AN H2O SUPPLEMENT**

For an animal which does not or cannot drink, H2O balance under conditions of restricted H2O is achieved when metabolic H2O production plus preformed food H2O intake equal evaporative H2O loss plus urinary and fecal H2O loss. If it is assumed that daily metabolizable energy intake equals daily energy metabolism,

\[
\frac{M_p}{c_s} g_s + M \sum \frac{q_i}{c_i} g_i + m_m
\]

and urinary and fecal H2O loss

\[
\frac{M_p}{c_s} l_s + M \sum \frac{q_i}{c_i} l_i
\]

(table A1 gives definitions and measured or estimated values for each symbol). In these equations \( \rho \) and \( q \) represent the proportions of daily energy requirements satisfied through consumption of the food which will be an H2O supplement (subscript \( s \) refers to this food) or other foods in the diet (subscript \( i \)), respectively \( \rho + \sum q_i = 1.0 \).

The total H2O balance equation is

\[
\frac{M_p}{c_s} g_s + M \sum \frac{q_i}{c_i} g_i + m_m = \frac{M_p}{c_s} l_s + M \sum \frac{q_i}{c_i} l_i + m_e .
\]

Rearranging to solve for the H2O content of the supplement \( g_s \) yields

\[
g_s = l_s + \frac{c_s}{\rho} \sum \frac{q_i}{c_i} (l_i - g_i)
\]

\[
+ \frac{c_s}{M_p} (m_e - m_m).
\]

<table>
<thead>
<tr>
<th>TABLE A1</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>LIST OF SYMBOLS AND THEIR MEASURED OR ESTIMATED VALUES FOR “AMMOSPERMOPHILUS LEUCURUS”</strong></td>
</tr>
<tr>
<td>Symbol</td>
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<td>( c )</td>
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<td>( \rho )</td>
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<tr>
<td>( q )</td>
</tr>
</tbody>
</table>

* \( m_m \) calculated as \( M \times .029 \) ml H2O (kJ metabolized)^{-1}.
LITERATURE CITED


