THE EFFECTS OF MOISTURE CONTENT AND METABOLIC WATER PRODUCTION
ON DESERT RODENT SEED PREFERENCES

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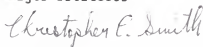Manhattan, Kansas

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DIET OPTIMIZATION BY A HETEROMYID RODENT: THE ROLE OF

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ABSTRACT

Kangaroo rats (family Heteromyidae) are primarily granivores.
These desert rodents do not drink free water, they instead depend
upon preformed water in their diet and the water produced by the
oxidation of food (metabolic water). The oxidation of different
nutrients produces different net amounts of metabolic water. At low
humidities, oxidizing carbohydrates produces a net metabolic water
gain whereas lipid metabolism requires the investment of more water
than is produced, resulting in a net water loss. Protein metabolism
produces a severe water loss, mainly through urination. Under humid
conditions, carbohydrate metabolism again produces a net water gain,
and although slightly reduced, protein metabolism still results in a
large water loss. Lipid oxidation at high humidities, however,
produces a large net metabolic water gain. Diet composition
therefore influences heteromyid water balance and accordingly may
also affect diet choice. Preference experiments involving
semi-synthetic diets were conducted to determine the influence of net
metabolic water production on the diet preferences of _Dipodomys_
spectabilis. Results indicate that at low humidities, kangaroo rats
in a positive water balance prefer: 1) intermeadiate protein, 2) high
lipid, and 3) high carbohydrate diets. When water stressed, the
rodents prefer low protein diets and the preference for high lipid
diets decreases. At high humidites, the rodents always prefer high
lipid diets. These results indicate that kangaroo rats usually
prefer diets that produce the greatest net metabolic water gain,
regardless of energy content.

INTRODUCTION

Kangaroo rats (family Heteromyidae) are mainly granivores, feeding on grass, forb and shrub seeds (Vorhies and Taylor 1922, Reynolds 1958, Bradley and Mauer 1971, Reichman 1975) and some species store large amounts of seeds in underground caches (Shaw 1934). Heteromyid rodents possess a number of physiological adaptations to desert environments that reduce water losses through urination, respiration and fecal production (MacMillen 1983). Kangaroo rats do not drink water, they instead depend upon preformed water in their diet and the metabolic water produced by food oxidation (Schmidt-Nielsen 1964, 1972), and thus seeds serve as a resource packet of both food and water for these rodents (MacMillen and Christopher 1975).

A number of studies have examined the seed species gathered and ingested by heteromyids (reviewed by Reichman and Price 1988), but the basis of their diet selection is poorly understood. An optimal diet is the one that maximizes fitness (Pyke et al. 1977). Conventional optimal foraging theory assumes that small homeotherms satisfy their nutritional requirements before meeting their energetic needs while foraging (Emlen and Emlen 1975). The optimal diet is thus the one that provides the greatest net energy gain and diet selection should be based primarily on energy content (Pyke et al. 1977, Krebs and McCleery 1984, Pyke 1984). Optimal foraging theory therefore suggests that the nutritional factor that is most limited in the diet should be the primary basis of diet choice. Herbivores

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generally maximize protein intake in addition to energy while foraging, mainly because protein is also limited in these systems (Mattson 1980), and some rodents that include seeds in their diets also maximize protein intake (Peters and Harper 1984, Yogoshi et al. 1986). Seeds are composed mainly of proteins, lipids (oils) and carbohydrates (Jones and Earle 1966). The carbohydrates found in seeds are mostly starches and the hexose (six-carbon sugar) glucose (Noggle and Fritz 1983). Seed energy contents range from 17.99 to 28.45 kJ/g depending upon species; the average energy content of grass seeds is 18.83 kJ/g and the mean for shrub seeds is 20.92 kJ/g (Robbins 1983). The average energy value of lipids is 39.54 kJ/g, proteins have a mean of 23.64 kJ/g, and carbohydrates average 17.70 kJ/g (Robbins 1983). Among the seeds normally ingested by kangaroo rats, those of high lipid or protein content will thus usually have a higher energy content those high in carbohydrates. If kangaroo rat fitness is most positively correlated with energy and protein intake as predicted by conventional foraging theory, they should: 1) maximize protein intake, 2) maximize lipid intake, and 3) minimize carbohydrate intake. This predicts that high lipid and protein seeds are preferred whereas high carbohydrate seeds are avoided.

The diet selection of some granivores is not based entirely on energy content, however (Smith and Follmer 1972, Pulliam 1980). Previous investigations of heteromyid diet selection do not support the energy maximization hypothesis of conventional optimal foraging theory. Examinations of the diets of free ranging <u>Dipodomys merriami</u>

and several pocket mouse species by Reichman (1977) indicate that heteromyids do not maximize energy intake. Laboratory experiments involving six heteromyid species and eight seeds species conducted by Price (1983) failed to demonstrate any influence of energy or protein content on seed selection. Investigations of _Dipodomys ordii_ in the field indicated energy content actually has a negative influence on seed choice, but a positive correlation existed between protein content and seed preference (Henderson 1985).

Most previous considerations of heteromyid seed selection have placed little emphasis on the possible role of water intake. In the desert, most seeds contain little preformed water (Chew 1965, Morton and MacMillen 1982). The energy content of seeds, in contrast, is relatively high and it appears that kangaroo rats can easily meet their energetic requirements on such a diet (Henderson 1985). Water thus appears to be more limited than energy in this system. I propose that net water intake is consequently more positively correlated with heteromyid fitness than energy intake and thus the optimal strategy is to maximize net water intake. Kangaroo rats may therefore prefer seeds that: 1) contain the most preformed water, and 2) produce the greatest net metabolic water gain when oxidized. Previous experiments have demonstrated that kangaroo rats prefer seeds of relatively higher water content and these results are · summarized elsewhere (Frank 1987a, Chapter II, this volume). A model for maximizing net metabolic water production is here developed and tested.

A model for maximizing net metabolic water production

The catabolism of all foodstuffs containing hydrogen produces oxidative water (Schmidt-Nielsen 1964). Food catabolism also results in obligatory water losses through urination, evaporation (respiration), and fecal production (Schmidt-Nielsen 1975). The net water gains or losses through food metabolism is thus the difference between the amount of oxidative water produced and the amount lost through catabolism, and these amounts in turn depend upon diet composition (Schmidt-Nielsen 1964, Hill 1976). Fecal production accounts for only 5% of the total water loss of kangaroo rats (Schmidt-Nielsen 1972), and thus when the diet contains some preformed water, fecal water loss is usually insignificant and need not be included in calculating net metabolic water production (Hill 1976). The net amount of metabolic water produced by oxidizing lipids or carbohydrates is therefore the difference between the oxidative water produced and the amount lost via evaporation. The amount of water lost through urination must also be considered when calculating the net water production from protein metabolism (Hill 1976).

The evaporative water loss of bannertail kangaroo rats (<u>Dipodomys spectabilis</u>) breathing dry air at 25°C and 20% relative humidity (RH) is 0.57 mg H_2O/mL O_2 consumed (Schmidt-Nielsen and Schmidt-Nielsen 1950a). Kangaroo rats have a maximum urine concentration of about 20% urea (Schmidt-Nielsen et al. 1948). The catabolism of 1 g of protein requires the excretion of 0.343 g of

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urea. Assuming a urine concentration of 20% urea, 1.458 g of water is required to void this amount of urea (Schmidt-Nielsen 1964). Using this information along with data on the oxidative water production and the oxygen consumption associated with the oxidation of starch, hexose, lipid and protein (Peters and VanSlyke 1946, Schmidt-Nielsen 1964), the net amount of water produced by _Dipodomys spectabilis_ oxidizing these nutrients while breathing dry (RH = 20%) air are calculated in Table 1. The amount of evaporative water lost was caluculated by multiplying the evaporative water loss by the amount of oxygen required for oxidation. Under these conditions, hexose oxidation produces the largest net gain in metabolic water. Starch oxidation also results in a net metaboic water gain, whereas lipid metabolism prouduces a net water loss (Table 1). Protein metabolism results in a substantial water loss, mainly through urination (Table 1).

To maximize net water intake, kangaroo rats should maximize carbohydrate intake and minimize protein and lipid intakes. Proteins and lipids, however, are important components of animal tissues and are therefore required in the diet (Robbins 1983). To maximize water intake, kangaroo rats may ingest only enough proteins and lipids to meet their minimal nutritional requirements. There is little information on the nutritional requirements of kangaroo rats, but the requirements of laboratory hamsters (_Mesocricetus auratus_) and gerbils (_Meriones unguicalatus_) are known. These rodents have physiological adaptations to desert conditions similar to those of

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kangaroo rats (Schmidt-Nielsen 1964, Buffenstein 1984), thus they probably have similar nutritional requirements. Hamsters require a diet of 5% lipid and 15% protein (Knapka and Judge 1974, Banta et al 1975), and gerbils diets must be 12% lipid and 16% protein (Harriman 1969, Arrington et al. 1973). Rodents also need carbohydrates in their diet, but no minimal requirement has been determined (NRC 1978). Using these values to estimate the requirements of kangaroo rats, it is predicted that they: 1) minimize protein intake to about 15% of the diet, 2) minimize lipid intake to 5-12% of the diet, and 3) maximize carbohydrate intake.

Some previous heteromyid seed preference studies support these predictons. Field experiments involving <u>Dipodomys deserti</u> suggest that low lipid-high carbohydrate seeds are preferred by these rodents (Lockard and Lockard 1971). A negative correlation between heteromyid seed choice and lipid content was demonstrated in the laboratory experiments conducted by Price (1983). Although the results of the study by Henderson (1985) suggest that <u>Dipodomys ordii</u> maximizes protein intake, it is important to note that most of the seeds available to the kangaroo rats in this study were less than 15% protein. These results therefore support the prediction that protein intake is maintained at 15% of the diet.

Evaporative water loss decreases as relative humidity increases (Christian 1978) and as temperature decreases (MacMillen 1983). Humidity and temperature thus both affect net metabolic water production. Although little data exists on the exact quantitative

effects of temperature and humidity on heteromyid evaporative water loss, modification of theoretical calculations by Schmidt-Nielsen and Schmidt-Nielsen (1951) estimates kangaroo rat evaporative water loss to be 0.326 mg H_2O/mL O_2 consumed in humid (RH = 66%) air at 25°C (D. Christian, personal communication). The net metabolic water production of kangaroo rats breathing humid air is calculated in Table 1 using this estimate. At this humidity, carbohydrate oxidation again results in a net water gain. Although somewhat reduced, protein metabolism still produces a substantial water loss, primarily through urination (Table 1). Lipid metabolism, however, no longer results in a net water loss and now produces the largest net water gain (Table 1). It is therefore predicted that under humid conditions (and/or low temperatures), high lipid-low carbohydrate diets are preferred, whereas protein preferences should be the same as before. Because only a crude estimate of evaporative water loss was employed in their calculation, the net metabolic water yields for humid air listed in Table 1 are for illustrative purposes only and should not be interpreted literally.

To test the diet preferences predicted by this model, a series of laboratory diet choice experiments involving semi-synthetic diets were conducted. It was predicted that kangaroo rats would prefer the diets that produce the largest net metabloic water gain regardless of energy content.

MATERIALS AND METHODS

Dipodomys spectabilis were used in the experiments. Thirty

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rodents were live-trapped near Portal, Arizona during November 1985. They were housed individually in plastic rats cages (50 by 25 by 30 cm) and maintained on a 12L:12D photoperiod at 25°C and 20% relative humidity in the laboratory. The rodents were fed a mixed seed diet supplemented with carrots as a water source.

The base of the semi-synthetic diets produced was finely ground husked barley seeds. Eight independent husked barley samples (one from each barley lot received) were chemically analyzed. Crude protein content was determined using the micro-Kjeldahl procedure, lipid content was assessed by ether extraction (VanSoest 1967). Glucose and starch contents were determined using a modification of the technique from Pramathesh and Tuorto (1984). The values obtained were averaged and these means are listed in Table 2 as the composition of the control diet. To produce diets of different protein contents, enough high nitrogen casein (United States Biochemical Corp.) was added to two 3 kg quantites of groung barley to make medium (15%) and high (20%) protein mixtures. This same procedure was followed using sunflower oil to produce medium (5%) and high (10%) lipid mixtures, glucose was added to make medium (3%) and high (6%) glucose mixtures, and corn starch was used to make the high (87%) starch mixture. Because preliminary experiments demonstrated that protein content affects kangaroo rat diet choice, enough casein was added to the lipid, glucose and starch mixtures to keep their protein content at 10%. Possible indirect effects on diet choice due

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the dilution of the protein content of the barley by adding oil, glucose or starch were thus avoided. Each mixture was homogenized in a laboratory "V" blender for 5 minutes. The mixture was then pressed into 0.1 g cylindrical feed pellets using a laboratory pellet mill at 60°C.

The calculated compositions of the diets are given in Table 2. The control diet is untreated ground barley that was pelleted. Diet energy contents were determined by analyzing two samples of each diet on an ash-free, dry matter basis with a Parr series 1411 semimicro calorimeter fitted with an AC5E semimicro oxygen bomb. The two values obtained for each diet were then averaged. The remainder of each diet not listed in Table 2 consists mainly of ash, fiber, and sugars other than glucose (C. Frank, unpublished data). Due to limitations in the pelleting process used, the highest lipid diet that could be produced was only 10% oil. For each set of diets, the range of compositions produced are within the range seen for the plant seed families used by heteromyids (Jones and Earle 1966).

All diet preference experiments were conducted at 25°C and about 20% relative humidity except for three lipid preference experiments which were performed at 25°C at 65% relative humidity in a Conviron model S10h enviromental chamber. To further detail the role of the estimated protein and lipid requirements in kangaroo rat diet choice, additional protein and lipid preference experiments were conducted after the rodents had been water stressed. Kangaroo rats were water

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stressed by maintaining them on a diet of 8 g of sunflower seeds per day for 3 days at 25°C and 20% relative humidity. Previous feeding trials demonstrated that the rodents could not maintain a positive water balance on a sunflower seed diet under these conditions. Additional feeding trials with sunflower seeds were conducted to confirm that this water stressing procedure did result in a negative water balance.

Only 30 kangaroo rats could be manitained due to laboratory equipment limitations. Each diet preference experiment involved 10 randomly selected animals. The rodents were allowed to recover for at least 2 weeks between experiments by feeding them their normal diet. All animals were familiarized with the diets prior to the experiments. Seven grams of each diet involved was offered to every subject in all preference experiments. This amount of food is slightly more than the rodent's daily requirement, as determined using a mass-based metabolic formula (Morton et al. 1980). An individual could therefore meet its requirement with only one diet. Diets were offered at the onset of darkness, each diet was placed in the cage in a separate pile at randomly determined positions. Remaining pellets were recovered after 12 h, sorted by diet type, weighed, and analyzed for water content.

The pellets were color coded for their diet type using commercial food colorings. Previous preference experiments with these diets revealed no significant preference for any color (Frank 1987b). The five colors used were rotated such that a particular diet was a

specific color only once in the study. Because moisture content influences kangaroo rat seed choice (Frank 1987a, Chapter II, this volume), all pellets were dried at $40°C$ for 24 h prior to presentation. Analyses of the diets at presentation revealed no significant differences in moisture content between them. Diet water contents ranged from about 6 to 8%.

Diet and sunflower seed moisture contents were determined using the techniques of Hart et al. (1959). The amount of each diet consumed was calculated as the difference between the amount of dry matter initially presented and the amount remaining. The diet intakes of experiments involving 3 different diets were compared using Friedman's analysis of variance by ranks, a non-parametric test, and Newman-Keul's procedure for ranked data was used to identify statisitcally different pairs of intakes (Zar 1974). A paired t test was used to compare the amounts consumed in the experiments involving only 2 diets (Snedecor and Cochran 1980).

Protein preference experiments

The kangaroo rats were presented with the control, medium and high protein diets in the first protein preference experiment. The control and high protein diets were offered in the second experiment since these diets were equally avoided in the first trial. The rodents were given the control, medium and high protein diets after being water stressed in the third experiment. A final protein preference trial where the rodents were water stressed and then offered the control and medium protein diets was performed.

Lipid preference experiments

The first lipid preference experiment involved the control, medium and high lipid diets. The control and medium lipid diets were offered in the second experiment since these diets were equally avoided in the first feeding trial. The third experiment involved control, medium and high lipid diets after water stress. In the fourth feeding trial, the rodents were offered the medium and high lipid diets after they had been water stressed; these diets were equally preferred in the third experiment.

The fifth, sixth and seventh lipid preference experiments were conducted under humid (RH = 65%) conditions to determine the effects of humidity on lipid preferences. The kangaroo rats (in their cages) were placed in the evironmental chamber 7 h prior to diet presentation in each experiment. The control, medium and high lipid diets were offered in the fifth experiment. The sixth feeding trial involved the control and medium lipid diets. The rodents were water stressed prior to being place in the environmental chamber in the seventh feeding trial. This experiment involved the control, medium and high lipid diets.

Carbohydrate preference experiments

The first carbohydrate preference experiment involved the control, medium and high glucose diets. The rodents were offered the control and medium glucose diets in the second experiment since they were equally avoided during the first trial. The final carbohydate preference experiment involved the control and high starch diets.

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Room temperatures during the experiments averaged 25°C with little variation (SE = 0.4, $\underline{n}$ = 8), and the mean relative humidity was 18.1% (SE = 0.9, $\underline{n}$ = 8). When the rodents were in the evironmental chamber, the temperature in the chamber was constant at 25°C and the mean relative humidity was 65.0% (SE = 5.3, $\underline{n}$ = 5). When water stressed the body mass of kangaroo decreases (Schmidt-Nielsen and Schmidt-Nielsen 1951). To confirm that the sunflower seed diet procedure used did result in water stress, two experiments examining the effects of sunflower seeds on body mass were conducted. In the first experiment, 10 kangaroo rats were fed 8 g of sunflower seeds per day for 3 days while being maintained at 25° C and 20% RH. Almost all seeds offered were ingested. The mean moisture content of the seeds was 4.78% (SE = 0.77, $\underline{n}$ = 9). The rodents had a mean body mass ($\pm$ SE) of 109.11 $\pm$ 5.18 g at the beginning of the experiment, but it significantly decreased to 105.50 $\pm$ 4.60 g by the end of the period (paired $\underline{t}$ test: $\underline{t}$ = 3.43, df = 9, $\underline{P}$ < .025). This suggests that the rodents were water stressed when fed this diet under dry conditions.

To determine if the observed body mass decrease was due only to water stress and not to other nutrtional factors, a second sunflower seed experiment was performed. Ten kangaroo rats were maintained at 25°C and 65% RH in an evironmental chamber and were fed 8 g of sunflower seeds per day for 3 days. The sunflower seeds used in this trial were incubated at 100% relative humidity and 35°C for 3 days

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prior to being fed to the rodents, which increased the mean water content of the seeds to 19.02% (SE = 0.29, $\underline{n}$ = 3). The mean initial body mass of the rodents was 111.23 $\pm$ 4.19 g and it significantly increased to 114.40 $\pm$ 4.29 g by the end of the experiment ($\underline{t}$ = 5.66, df = 9, $\underline{P}$ < .01). This indicates that the body mass loss associated with the sunflower seed diet in dry air is due soley to a negative water balance.

Protein preference experiments

In the first protein preference experiment, the kangaroo rats ingested significantly more of the medium protein diet than of the control and high protein diets (Fig. 1A), which were equally avoided ($\underline{X}^2$ = 9.80, df = 2, $\underline{P}$ = .01). The control and high protein diets were equally ingested when they were offered in the second experiment ($\underline{t}$ = 0.72, df = 9, $\underline{P}$ = .45; Fig. 1B). The rodents preferred the control and medium protein diets over the high protein diet (Fig. 1C) when water stressed in the third feeding trial ($\underline{X}^2$ = 7.14, df = 2, $\underline{P}$ < .05). After water stress in the fourth experiment, the rodents ingested significantly more of the control diet than of the medium protein pellets ($\underline{t}$ = 9.75, df = 6, $\underline{P}$ = .001; Fig. 1D).

Lipid preference experiments

Significantly more of the high lipid diet was consumed than of the control and medium lipid diets, which were ingested equally (Fig. 2A), in the first lipid preference experiment (X^2 = 15.00, df = 2, $\underline{P}$ < .005). Over 10 times as much of the medium lipid diet was ingested than the control pellets in the second experiment ($\underline{t}$ =

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22.00, df = 9, $\underline{P}$ = .001; Fig. 2B). After water stress in the third experiment, the rodents significantly preferred the medium and high lipid diets over the control diet ($\underline{X}^2$ = 9.25, df = 2, $\underline{P}$ < .01; Fig. 2C). There was no significant difference between that amounts of the medium and high lipid diets eaten (Fig. 2D) when these diets were offered after water stress in the fourth feeding trial ($\underline{t}$ = 1.07, df = 8, $\underline{P}$ = .35). When under humid conditions in the fifth experiment, the kangaroo rats ingested statistically eqivalent amount of the control and medium lipid diets (Fig. 2E) and significantly preferred the high lipid diet over the other diets ($\underline{X}^2$ = 6.33, df = 2, $\underline{P}$ < .05). Twice as much of the medium lipid diet than of the control diet was consumed (Fig. 2F) under humid conditions in the sixth experiment ($\underline{t}$ = 2.54, df = 8, $\underline{P}$ = .03). Water stress in the seventh experiment did not affect the lipid preferences observed at high humidites; significantly more of the high lipid diet was ingested than of the control and medium lipid diets (Fig. 2G) and more of the medium lipid diet was consumed than of the control diet ($\underline{X}^2$ = 16.22, df = 2, $\underline{P}$ < .005). Seeds in high humidities gradually imbibe water (Morton and MacMillen 1982, Christian and Lederle 1984), thus the diet preferences observed under humid conditions may have been due to differences in diet water content. This possibility was examined by determining the moisture contents of 3 samples of each diet taken both at the beginning and end of the seventh lipid preference experiment. The mean moisture contents ($\pm$ SE) of the control, medium and high lipid diets at the beginnig of the

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experiment were 7.67 ± 0.06, 7.84 ± 0.10, and $7.59 \pm 0.16\%$ respectively, and were not siginifcantly different (ANOVA: $\underline{F} = 1.18$, df = 2,6, $\underline{P}$ = .37). The mean moisture contents increased during the experiment to 15.26 ± 0.16, 14.76 ± 0.14, and $16.02 \pm 0.15\%$ respectively, but were still statisically equivalent ($\underline{F} = 3.84$, df = 2,6, $\underline{P}$ = .08). The diet preferences observed at high humidities were thus not due to differences in diet water content.

Carbohydrate preference experiments

The high glucose diet was preferred over the control and medium glocose diets (Fig. 3A) in the first carbohydrate preference experiment ($\underline{X}^2 = 13.40$, df = 2, $\underline{P} < .005$). Significantly more of the medium glucose diet was consumed than of the control diet when these diets were presented in the second experiment ($\underline{t} = 2.95$, df = 7, $\underline{P} < .025$; Fig. 3B). The high starch diet was significantly preferred over the control diet (Fig. 3C) during the final carbohydrate preference experiment ($\underline{t} = 2.49$, df = 6, $\underline{P} < .05$).

DISCUSSION

The observed diet preferences demonstrate that kangaroo rats prefer those diets which produce the greatest net amount of metabolic water, subject to nutritional constraints. The rodents normally preferred the 15% protein diet, as predicted, and total dietary protein intake was kept at 15% by ingesting equal amounts of the 10 and 20% protein diets when the 15% protein diet was not available. When water stressed the rodents minimized protein intake by preferring the control (10% protein) diet, presumably because most

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animals can tolerate protein stress longer than water stress (Robbins 1983).

The kangaroo rats maximized lipid intake by preferring the 10% lipid diet when in a positive water balance and breathing dry air. When water stressed, however, the rodents reduced their lipid consumption by ingesting equal amounts of the 5 and 10% lipid diets. The lipid requirements of kangaroo rats may be as much as 12%, thus the rodents probably preferred the high (10%) lipid diet when in a positive water balance in order to satisfy their lipid need. Lipid consumption was reduced to conserve water when the animals were water stressed. The lipid requirement of kangaroo rats may also be as low as 5%, however. This suggests that the high lipid diet was preferred because rodents normally maximize lipid intake. The additional energy gained by ingesting high lipid diets may outweigh the small water loss associated with these diets. Lipid intake may be minimized as predicted only when the animals are water stressed. Only experiments involving diets with lipid contents higher than 10% can determine which of these explainations is correct. Repeated attempts at producing very high lipid diets using the methods described earlier failed to produce usable diets, presumably due to the hydrophobic properties of plant oils. The results of this study indicate, however, that kangaroo rats minimize lipid intake under at least some circumstances.

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The rodents preferred high lipid diets under humid conditions. Instead of reducing the preference for high lipid diets as seen in dry air, water stress actually enhanced this preference under humid conditions. This demonstrates that lipid intake is always maximized under humid condtions, as predicted. The kangaroo rats maximized glucose and starch consumption when breathing dry air, which supports the prediction that the rodents maximize carbohydrate intake.

The results also indicate that heteromyid diet choice is often not based on energy content. The rodents normally preferred the medium protein diet over the high protein diet, even though it has a lower energy content (Table 2). Although having a lower energy content (Table 2), the rodents preferred the high starch diet over the control diet. Energy content influences diet choice even less when the rodents are water stressed. The control diet has a lower energy content than the medium and high protein diets (Table 2), yet it is preferred over these diets after water stress. The medium and high lipid diets were equally preferred under these conditions despite the higher energy value of the high lipid diet (Table 2).

The diet preferences of kangaroo rats with respect to both metabolic water and preformed water contents demonstrate that the optimal diet for heteromyid rodents is the one that maximizes water intake and meets minimal nutritional requirements. Water is the major currency upon which seed selection is based. Energy intake is maximized only when this also maximizes net water gain or when the negative effects on water balance are slight. Because the strategy

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of kangaroo rat diet selection apparently is to maximize overall water intake, total seed water content (preformed + metabolic) must be considered when examining heteromyid seeds preferences.

The foraging strategy of kangaroo rats appears to be risk aversive and time minimizing (Schroder 1979, Henderson 1985). The rodents are noctural, spending a total of only 1 to 3 h per night foraging outside of their burrows (Kenagy 1973, Schroder 1979, Braun 1985) by quickly filling their cheek pouches during rapid and short forays (Shaw 1934, Tappe 1941). Seeds are eaten inside the burrow, therefore diet selection apparently takes place in the burrow as well. The observed diet preferences therefore indicate the order and proportion in which gathered and stored seeds are eaten, but they are probably not the primary basis on which seeds are gathered.

The demonstrated influences of water balance and humidity on kangaroo rat diet choice suggest that it may vary with season as predicted by MacMillen and Hinds (1983). The burrows of D. spectabilis are cooler and more humid that the above-ground environment during the summer, but the average temperature inside them is 29°C and the mean relative humidity is only 31% (Schmidt-Nielsen and Schimdt-Nielsen 1950b). In the summer, consequently, the evaporative water loss of the rodents approaches metabolic water production, resulting only in a marginal net . metabolic water gain, and the animals concentrate their urine as much as possible during this period to conserve water (MacMillen and Chritopher 1975). Lipid and protein intakes may thus be limited to

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minimal requirements in the summer. Although free ranging kangaroo rats are normally in a positive water balance (MacMillen and Christopher 1975), the rodents may be occaisionally water stressed during the summer when conditions are particularly severe. The rodents may even consume less than their minimum protein and lipid requirements during these periods as seen when the rodents were water stressed in this study.

The internal temperature of kangaroo rat burrows during the winter is usually between 4 and $11°C$ (Kenagy 1973) and their humidity is constantly close to or at saturation (Kay and Whitford 1978). The evaporative water loss for kangaroo rats in the winter is therefore greatly reduced, producing a substantial net metabolic water gain, and the rodents no longer concentrate their urine (MacMillen and Christopher 1975). Lipid intake may thus be maximized during this season, taking advantage of the additional energy sources that can now be consumed, as seen in the lipid preference tests under humid conditions. Protein consumption, however, probably is still minimized to 15% of the diet due to the water loss through urination.

To understand heteromyid seed selection in the field, the diet preferences demonstrated in this study need to be further investigated at various temperatures and humidites. This requires that the effects of temperature, humidity, and their interactions on heteromyid evaporative water loss be further detailed. A number of desert-dwelling birds and mammals, in addition to heteromyids, rely on their diet for water (Robbins 1983). Many non-desert animals,

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such as squirrels (Smith 1968) gophers (Vaughan 1967) and most insects (Chapman 1982), also depend on their diet for water. Further investigation of heteromyid diet choice will thus undoubtedly provide additional insight in the feeding behavior of a variety of organisms.

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TABLE 1. Net amounts of metabolic water produced by the oxidation of various nutrients by _Dipodomys spectabilis_ breathing dry (RH = 20%) and humid (RH = 66%) air at 25 C.

Nutrient class	Water produced by oxidation* (g H_2O/g)	Oxygen required for oxidation* (mL O_2/g)	Dry air		Humid air	
			Evaporative water lost (g H_2O/g)	Net metabolic water yield (g H_2O/g)	Evaporative water lost (g H_2O/g)	Net metabolic water yield (g H_2O/g)
Starch	0.556	828	0.472	0.084	0.270	0.286
Hexose	0.600	746	0.425	0.175	0.243	0.357
Lipid	1.071	2019	1.151	-0.080	0.658	0.413
Protein	0.396	967	0.551	-1.613[+]	0.315	-1.377[+]

* From Peters and VanSlyke 1946, Schmidt-Nielsen 1964.

[+] Including 1.458 g of water lost through urination.

TABLE 2. Nutritional composition of the semi-synthetic diets.

Diet	Protein	Lipid	Starch	Glucose	Energy Content (kJ/g)
Control	10.0	2.0	82.0	1.0	18.07
Medium protein	15.0	1.8	76.9	0.9	18.32
High protein	20.0	1.6	69.7	0.8	18.78
Medium lipid	10.0	5.0	78.8	0.9	18.62
High lipid	10.0	10.0	74.2	0.8	20.09
Medium glucose	10.0	1.9	80.8	3.0	18.18
High glucose	10.0	1.8	78.4	6.0	18.31
High starch	10.0	1.3	87.0	0.7	18.01

FIG. 1. Histgrams indicating the mean ($\pm$ SE) intake per subject (g) of each diet in the protein preference experiments. The abcissa indicates diets which are control (10% protein), medium (15%), and high (20%) protein. The ordinate is the mean amount consumed per subject. Those bars within an experiment sharing a common letter are statistically equivalent at the $\underline{P}$ = .05 level.
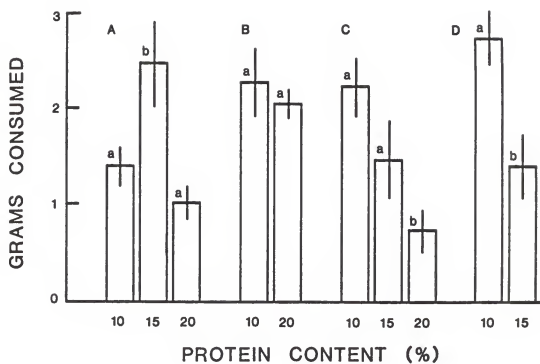
FIG. 2. Histograms indicating the mean ($\pm$ SE) intake per subject of each diet in the lipid preference experiments. The abscissa indicates diets which are control (2% lipid), medium (5%), and high (10%) lipid. The ordinate is the mean amount consumed per subject. Those bars within an experiment sharing a common letter are statistically equivalent at the $\underline{P}$ = .05 level.
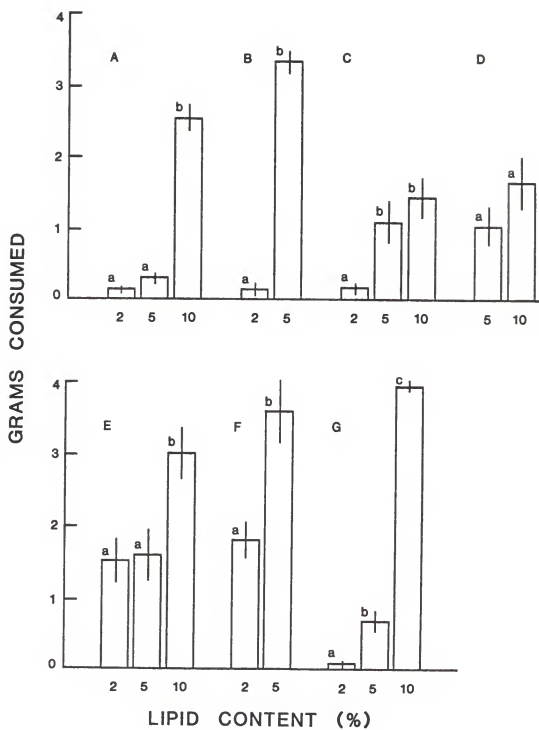
FIG. 3. Histograms indicating the mean ($\pm$ SE) intake per subject of each diet in the carbohydrate preference experiments. The abscissa indicates diets which are control (1% glucose, 82% starch), medium (3%) glucose, high (6%) glucose, and high (87%) starch. The ordinate is the mean amount consumed per subject. Those bars within an experiment sharing a common letter are statistically equivalent at the $\underline{P}$ = .05 level.
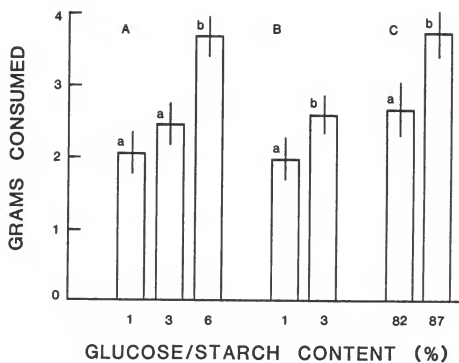
II.

DIET OPTIMIZATION BY A HETEROMYID RODENT: THE ROLE OF MOISTURE

CONTENT

Abstract. Kangaroo rats are mainly granivores and some species store large amounts of seeds in underground caches. These desert rodents do not drink free water; they instead rely on preformed water in their diet and metabolic water produced by food oxidation. Moisture content may therefore influence kangaroo rat optimal seed selection. Feeding experiments were conducted to determine both the effects of water content on _Dipodomys spectabilis_ seed preferences, and the minimal water requirements of these rodents. Results indicate that kangaroo rats always prefer the moistest seeds available and they respond to very small differences in seed moisture content. The results also demonstrate that these rodents do not ingest only enough preformed water to meet their minimal requirements, as conventional foraging with nutrient constraint models predict, but instead always maximize water intake through their seed preferences.

Introduction

Kangaroo rats (family Heteromyidae) are primarily granivores, feeding mostly on desert grass, forb and shrub seeds (Vorhies and Taylor 1922; Reynolds 1958; Reichman 1975), and some species store large quantities of seeds in underground burrows (Shaw 1934). Heteromyids have physiological adaptations to desert environments that reduce water losses through urination, respiration and fecal production (MacMillen 1983). These rodents do not drink water; they instead depend on preformed water in their diet and metabolic water produced by food oxidation. Seeds thus serve as a source of both food and water for kangaroo rats (MacMillen and Christopher 1975).

The amount of metabolic water produced by food oxidation alone often cannot compensate for all kangaroo rat water losses, thus the diet must also contain some minimal amount of preformed water for the rodents to achieve a positive water balance (Schmidt-Nielsen and Schmidt-Nielsen 1951; MacMillen and Hinds 1983). Seed moisture content depends on relative humidity, generally increasing as humidity elevates, and is thus highly variable (Schmidt-Nielsen 1964; Morton and MacMillen 1982; Christian and Lederle 1984). Seed preference experiments involving _Dipodomys merriami_ demonstrated that this kangaroo rat species prefers seeds of relatively higher moisture content and can detect differences in water content as small as 10% of dry mass (Frank 1987a). Laboratory feeding trials with _Dipodomys spectabilis_ indicated that these kangaroo rats prefer diets which result in the greatest net metabolic water gain, thereby maximizing

metabolic water intake (Chapter I, this volume). Preformed water intake may also be maximized by kangaroo rats.

The optimal diet is the one which maximizes fitness (Pyke et al. 1977). Fitness is difficult to measure directly, so conventional optimal foraging theory often assumes that the diet which provides the greatest net energy gain is the optimal diet. Diet selection is thus normally based on energy content (Pyke et al. 1977; Krebs and McCleery 1984; Pyke 1984). If a required nutrient other than energy is limited, however, optimal diet models assume that there is a negative relationship between the amount of the required nutrient in the diet and its energy content (Pulliam 1975; Belovsky 1978; Rapport 1980). Once the animal has met its minimal nutritional requirement, therefore, further intake of the nutrient has no advantage. The optimal diet in this case is the one that contains only enough of the nutrient to satisfy minimal nutritional requirements, thereby maximizing net energy intake as much as possible while still meeting the nutritional requirement (Pulliam 1975; Belovsky 1978). Field studies of moose (_Alces alces_), for example, demonstrated that they ingest only enough aquatic vegetation, which is high in sodium and low in energy, to meet their minimal sodium requirement. The rest of their diet consists of high energy-low sodium terrestrial plants (Belovsky and Jordan 1978).

Among different seed species, energy content is inversely related to the amount of water the seeds will imbibe, mainly due to the hydrophobic nature of high energy lipids (Christian and Lederle

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1984). After a period of time, water uptake reduces seed energy content through germination (Noggle and Fritz 1983). Seed water uptake may also reduce the rate of kangaroo rat energy intake by increasing seed bulk proportionally. Conventional diet optimization theory thus predicts that kangaroo rats should ingest only enough preformed water through their seed preferences to meet their minimum water requirements.

The energy content of seeds is generally high (Robbins 1983), and the average energetic digestive efficiency of kangaroo rats is 94% (Schreiber 1979). Kangaroo rats can therefore easily meet their minimal energetic requirements on a seed diet (Henderson 1985). In contrast, most seeds contain little preformed water under desert conditions (Chew 1965; Morton and MacMillen 1982). Water appears to be more limited than energy in this system. The optimal strategy may be to maximize water intake rather than energy. Kangaroo rats may consequently maximize preformed water intake rather than limit it as predicted by conventional models.

A series of experiments involving _Dipodomys_ _spectabilis_ and seeds imbibed to different moisture contents was conducted to further explore the role of moisture content in kangaroo rat diet choice. It was predicted that kangaroo rats maximize preformed water intake.
Materials and methods

Twenty-five _D_. _spectabilis_ were live trapped near Portal, Arizona, during August 1984. Each animal was housed in the laboratory in a seperate plastic cage (50 by 25 by 35 cm) that

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contained a 1.5 cm layer of sand on the bottom and had a screen top. The rodents were maintained at 25°C and 20% relative humidity on a 12:12 light:dark cycle and fed a diet of mixed seeds and carrots.

Seeds in high humidities gradually imbibe water over a period of days (Morton and MacMillen 1982; Christian and Lederle 1984). To produce seeds of different water contents, husked barley seeds were incubated in individual 7 g (dry mass) quantites at 35°C and 100% relative humidity for various periods. They were placed on screens over 150 ml of water in 1 gallon jars that were sealed. Commercial grains are usually inoculated with ubiquitous fungal spores during storage and will become moldy under humid conditions (Martin and Gilman 1976). All seeds were therefore surface sterilized with 300 kilorads of gamma radiation prior to incubation and all materials used for incubation were autoclaved, since moldiness affects kangaroo rat seed choice (Frank 1987b). Dry seeds were produced by drying non-imbibed seeds at 55°C for 24 h.

Preformed water requirement experiments

To examine the relationship between kangaroo rat moisture preferences and their preformed water requirement, the minimal water requirement under specific conditions must first be determined. Kangaroo rat body mass decreases when the rodents are water stressed (Schmidt-Nielsen and Schmidt-Nielsen 1951). Two experiments examining the effects of seed moisture content on body mass were conducted. In the first experiment, 5 animals were fed 7 g (dry mass) of non-imbibed barley seeds per day for 4 days. The rodents

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were maintained at 25°C and 20% relative humidity and weighed daily during this period.

The second experiment also involved 5 rodents that were fed 7 g of seeds per day for 4 days while being maintained at 25°C and 20% humidity. The seeds offered in this experiment were first incubated for 1 day and then allowed to air-dry for 12 h prior to being fed to the rodents. Previous seed incubation and drying experiments revealed that this procedure produced seeds with a stable moisture content only slighlty above that of non-imbibed seeds (Frank, unpublished data).

Seed preference experiments

Six seed preference experiments, each involving 10 animals, were conducted. The rodents were presented with 2 moisture levels below the estimated requirement (10.59% wet mass, see Results) in the first experiment by offering dried and non-imbibed (not incubated) seeds. Three moisture contents above the required amount (incubations for 1, 2, and 3 days) were offered in the second experiment. The rodents were given a choice between 1- and 2-day imbibed seeds in the third experiment since these treatments were equally avoided in the second trial.

Since increasing seed moisture content may reduce the rate of energy intake for the rodents, they may reduce preformed water intake when energy (food) stressed. The effects of energy stress on the moisture level preferred was determined by fasting the rodents for 24 h prior to the fourth, fifth and sixth preference experiments. The

rodents were presented with dried and non-imbibed seeds in the fouth experiment, 1-, 2-, and 3-day imbibed seeds in the fifth, and 1- and 2-day seeds in the sixth preference experiment. Because the rodents rely on their diet for water, severe food stress may also result in water stress which in turn may affect the preferred moisture level. Preliminary fasting experiments revealed, however, that fasting the rodents for only 24 h did not significantly affect their water balance (Frank, unpublished data).

All preference experiments were conducted at 25°C and 20% relative humidity. Previous experiments with imbibed seeds indicated that once removed from incubation, they slowly loose moisture via evaporation so that after about 4 h, all treatments will contain equivalent amounts of water (Frank 1987a). The rodents were thus allowed to feed for only 4 h in each experiment. The seeds were color coded for their treatment prior to incubation using commercial food colorings. The rodents have no significant preference for any particular color (Frank 1987b). The five dyes used were rotated such that a specific treatment was a particular color in only one of the experiments. All sand and remaining food was removed for the cages prior to the presentation of the experimental seeds. Experimental seeds were offered at the onset of darkness. To familiarize the rodents with the moisture levels, they were pre-fed the night before the first, second and third experiments with seeds of all treatments involved, and were pre-fed the night before they were fasted (2 nights before the experiment) in the fourth, fifth and sixth

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experiments. Seven grams (dry mass) of each treatment were offered
in all experiments. This amount is slightly more than the rodent's
daily requirement, as determined using a mass based metabolic forumla
(Morton et al. 1980). The seed treatments were placed in the cages
in seperate piles at randomly determined positions. All remaining
seeds after 4 h were collected, sorted by treatment, weighed and
analyzed for moisture content.

The treatments differed in water content and consequently wet
mass, therefore the amount of dry matter ingested was used to
determine seed preferences to avoid any biases. Treatment water
contents were determined at the start and end of each experiment
using the techinque of Hart et al. (1959) and were calculated as
percent of wet mass. The quantity consumed of each treatment was
calculated as the difference between the amount of dry matter
presented and that remaining.

Because only 25 rodents were available, the same 10 animals (6
female, 4 male) were used in the first 3 preference experiments, and
another group of 10 (6 female, 4 male) were used in the remaining 3
preference experiments. The 5 remaining rodents (3 female, 2 male)
were used in the water requirement experiments and digestibility
assays. In all cases, the rodents were allowed to recover for at
least one week between experiments on their normal diet. The intakes
of experiments involving 3 treatments were compared using Friedman's
analysis of variance by ranks, and Newman-Keul's procedure for ranked
data was used to identify statistically different pairs of intakes

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(Zar 1974). Standard ANOVA in conjunction with Tukey's Studentized Range was used to analyze differences in seed water content (Snedecor and Cochran 1980). Intakes of experiments involving 2 treatments were compared using a paired t test and the moisture contents were analyzed using the Student's t test (Snedecor and Cochran 1980).

Seed composition analyses

Non-imbibed and 3-day imbibed seeds were chemically analyzed to determine if the employed incubation procedure produced any changes in seed composition, other than in moisture content, that may have influenced seed choice. Crude protein content was determined using the micro-Kjeldahl procedure, and lipid content was assessed through ether extraction (VanSoest 1967). Carbohydrate content was determined using a modification of the technique from Pramathesh and Tuorto (1984). Four non-imbibed and five 3-day imbibed seed samples each were analyzed for protein, lipid and carbohydrate contents. Ash content was measured by burning preweighed samples (4 per treatment) at 500°C in a muffle furnance for 30 minutes (Paine 1971). Energy content of seed samples (3 per treatment) was measured on a dry matter, ash-free basis with a Parr series 1411 semimicro calorimeter.

Digestibility was determined by maintaining 5 rodents on non-imbibed and 3-day imbibed seeds for 72 h at 25°C and 20% relative humidity. They were fed 7 g (dry mass) of the test seeds per day, and all remaining seeds and feces produced were collected daily. Two feces samples per rodent were analyzed for energy content using the Parr 1411 calorimeter. Digestibility for each animal was calculated

as the fraction of the total energy consumed not lost in the feces

(Robbins 1983). Compositions were compared at each level using the

Student's t test.

Results

Preformed water requirement experiments

The mean moisture content ($\pm$ SE) of the non-imbibed seeds

presented in the first experiment was $9.63 \pm 0.22\%$ (N = 8). Mean

kangaroo rat body mass decreased throughout the experiment (Fig. 1)

such that the mean body mass at the end of the trial was

siginficanlty lower than that at the start (Paired t test: t = 15.73,

d.f. = 4, P < 0.001), indicating a negative water balance. The mean

moisture content of the 1-day imbibed, 12 h dried seeds presented in

the second experiment was $10.59 \pm 0.23\%$ (N = 8) and this is

significantly higher than that of the non-imbibed seeds used in the

first trial (t = 2.89, d.f. = 15, P = 0.01). Mean body mass remained

relatively constant during the experiment (Fig. 1) and there was no

siginificant difference between the intial and final body masses (t =

0.98, d.f. = 4, P = 0.30). The rodents ate virtually all the seeds

presented during both experiments. The minimal amount of preformed

water required is therefore estimated to be about 10.59% of the

diet. It should be noted, however, that because the rate of water

loss depends on diet composition (Hill 1976), humidity (Christian

1978), temperature (MacMillen and Hinds 1983), and heteromyid species

(Schmidt-Nielsen 1964), this estimate is applicable only to $\underline{D}$.

spectabilis on a barley seed diet under these conditions.

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Seed preference experiments

The dried and non-imbibed seeds offered in the first preference experiment differed siginificantly in moisture content at the start (t = 42.70, d.f. = 8, P = 0.0001) and end of the trial (t = 16.85, d.f. = 4, P = 0.0001), and the moisture contents were below 10.59% (Table 1). The rodents significantly preferred the non-imbibed seeds (Fig. 2A), ingesting over twice as much of them as the dried group (t = 2.87, d.f. = 9, P < 0.02). The 1-, 2-, and 3-day imbibed seeds presented in the second experiment all significantly differed in water content at the beginning of the trial (F = 34.21, d.f. = 14, P = 0.001), but their moisture contents converged during the experiment (Table 1) so that by the end of it, the water contents were statistically equivalent (F = 1.53, d.f. = 8, P = 0.29). The moisture contents of all treatments, however, were always above 10.59% (Table 1). The kangaroo rats significantly preferred the 3-day imbibed seeds over both the 1- and 2-day seeds (Fig. 2B), which were equally consumed (X^2 = 12.50, d.f. = 2, P < 0.005). The two incubation regimes offered in the third experiment, 1- and 2-day, significantly differed in moisture content at both the start (t = 5.07, d.f. = 8, P = 0.0005) and end (t = 3.60, d.f. = 3, P = 0.04) of the trial (Table 1). The rodents ingested significantly more of the 2-day treatment (Fig. 2C) than of the 1-day seeds (t = 3.61, d.f. = 9, P < 0.025).

In the fourth preference experiment, the dried and non-imbibed seeds had significantly different moisture contents at the start ($t = 46.37$, d.f. = 8, P = 0.001) and conclusion ($t = 7.82$, d.f. = 4, P = 0.01; Table 1). Fasting the rodents prior to this trial did not affect the moisture level chosen; they consumed over 3 times as much of the non-imbibed treatment (Fig. 2D) as the dried group ($t = 4.05$, d.f. = 9, P < 0.005). The 1-, 2-, and 3-day imbibed seeds used in the fifth experiment significantly differed in moisture content at the beginning ($F = 649.26$, d.f. = 14, P = 0.0001) and end of the experiment ($F = 116.80$, d.f. = 8, P = 0.001; Table 1). Fasting the rodents in this experiment also did not affect the preferred moisture level; they ingested significantly more of the 3-day seeds (Fig. 2E) than of the 1- and 2-day groups, which were equally consumed ($X^2 = 10.17$, d.f. = 2, P < 0.025). The moisture contents of the 1- and 2-day imbibed seeds in the last experiment were statistically different at the start of the trial ($t = 23.62$, d.f. = 8, P = 0.0001), but converged during the experiment (Table 1) so that by the conclusion, they were statisically equivalent ($t = 2.07$, d.f. = 2, P = 0.17). The kangaroo rats consumed significantly more of the 2-day treatment than of the 1-day seeds ($t = 3.63$, d.f. = 9, P < 0.01; Fig. 2F).

Seed composition analyses

The 3-day imbibed treatment contained significantly more water than the non-imbibed seeds ($t = 28.89$, d.f. = 4.5, P = 0.0001; Table 2). The non-imbibed and 3-day imbibed seeds did not significantly

differ in protein (t = 0.01, d.f. = 7, P = 0.99), lipid (t = 0.85, d.f. = 3.2, P = 0.45), carbohydrate (t = 0.22, d.f. = 7, P = 0.83), ash (t = 0.45, d.f. = 6, P = 0.67) and energy contents (t = 1.11, d.f. = 4, P = 0.33; Table 2). The digestibilities of both treatments were high (Table 2) and statistically equivalent (t = 0.29, d.f. = 8, P = 0.78).

Discussion

The results clearly demonstrate that like _Dipodomys merriami_, _D. spectabilis_ prefers those seeds containing relatively more water and can detect small differences in moisture content. The rodents preferred the moistest seeds available when the seeds offered contained less than the required amount of moisture, and when presented with those containing more than the minimal requirement. This demonstrates that kangaroo rats maximize preformed water intake rather than restricting it to the minimal amount needed. Preformed water intake was maximized both when the rodents were energy stressed and when they were not, indicating that the preference for moist seeds is independent of energy balance. The observed seed preferences were based solely on differences in water content since the non-imbibed and imbibed seeds analyzed did not significantly differ in chemical composition (other than moisture content) or digestibility.

Laboratory experiments conducted by Soholt (1977) with _D. merriami_ involving rolled oats and carrots also demonstrated that kangaroo rats maximize preformed water intake. The carrots used were

85% water, the remainder being mostly indigestible carbohydrates. The rolled oats were 7% water and the only source of the foodstuffs (proteins, lipids, carbohydrates, etc.) needed by kangaroo rats. The rodents could maintain a positive water balance on a diet of rolled oats alone, yet when offered both oats and carrots, they consumed slightly more carrots than oats. As a result, preformed water constituted about 50% of the total diet, almost 7 times more water than needed. The water content of desert grasses is 70 to 90% wet mass (Chew 1965; Robbins 1983). When available in the spring and early summer, green vegetation comprises 34 to 60% of the total diet of free ranging heteromyids (Bradley and Mauer 1971; Soholt 1973; Reichman and Van De Graff 1975). This indicates that free ranging kangaroo rats also consume more than the minimal amount of preformed water needed.

Kangaroo rats, like most mammals, do not store excess water, thus extra water consumed is voided after some time (Schmidt-Nielsen 1964). As Fig. 1 illustrates, consuming very dry seeds may result in a profound net water loss. Because under desert conditions most seeds contain little moisture, seeds containing sufficient amounts of water may be periodically rare. The best strategy may consequently be to maximize preformed water intake at all times in order to minimize the probability of water stress when moist seeds are scarce, since water cannot be stored for long periods. Consuming excess preformed water, when available, also enables the rodents to eat seeds that are nutritious, yet contain insufficient amounts of water,

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without incurring a negative water balance. By ingesting seeds that contain excess water, therefore, the rodents can expand their diet to include dry seeds that they otherwise could not exploit.

Kangaroo rats have a maximum urine concentration of about 20% urea; almost 5 times that of most mammals (Schmidt-Nielsen 1964). The rodents must concentrate their urine this much when feeding on dry seeds in order to remain in a positive water balance (Schmidt-Nielsen and Schmidt-Nielsen 1951). Urine concentration by the kidneys is an active process (Pitts 1968), thus producing highly concentrated urine requires the investment of considerable energy. When the moisture content of the diet increases, however, heteromyid urine concentration decreases proportionally (MacMillen and Christopher 1975). Maximizing preformed water intake thus also has the benefit of reducing the energy invested in urine concentration, and this may outweigh any energetic losses associated with preferring moist seeds.

Examinations of the diets of free ranging $\underline{D}$. merriami and several pocket mouse species by Reichman (1977) indicated that heteromyids do not maximize energy intake. Laboratory experiments involving six heteromyid species and eight seed species failed to demonstrate any influence of energy content on seed choice (Price 1983). Studies of free ranging Dipodomys ordii demonstrated that energy content actually has a negative effect on seed selection in this species (Henderson 1985). As mentioned earlier, preferring moist seeds may reduce energy intake. The preference for seeds that produce the greatest

net metabolic water gain when oxidized also reduces energy intake (Chapter I, this volume). The currency on which optimal diet selection is based depends on the biology of the organism being considered (Pyke et al. 1977). These studies indicate the major currency upon which heteromyid seed choice is based is water, not energy. The optimal strategy appears to be to maximize overall water intake, thus total seed water content (preformed + metabolic) must be considered when examing heteromyid diet selection.

Although most seeds on the desert surface usually contain little moisture (Morton and MacMillen 1982), kangaroo rat burrows are normally much more humid than the above-ground environment (Schmidt-Nielsen and Schmidt-Nielsen 1950; Kay and Whitford 1978), thus seeds stored within them will probably imbibe water. Kangaroo rats store dry seeds preferentially in areas of high relative humidity, apparently to increase their water content (Reichman et al. 1986). Kangaroo rat seed caches are sometimes so moist that the seeds stored within them germinate (Reynolds 1958). Caches may therefore be an important source of moist seeds for the rodents. The preference for moist seeds suggests the sequence of cache use. Those seeds that have been stored for some time, and thus contain more water, may be preferred by the rodents over those which have been recently gathered. Kangaroo rats may be unique among food caching animals in that the nutritional quality of their food increases with storage. The quality of food items in the caches of all other animals investigated either remains constant over time, or decreases

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through spoilage and through germination when seeds are stored (Smith and Reichman 1984; Sherry 1985).

Kangaroo rats forage above-ground for only a few hours per night (Kenagy 1973; Braun 1985) by quickly filling their cheeck pouches during short forays from their burrows (Tappe 1941). Seeds are ususally eaten inside the burrow, thus diet selection may take place inside the burrow as well. Because seed moisture content probably changes once inside the burrow and this may also be where diet selection takes place, above-ground seed selection may not be based on water content. Above-ground seed gathering may instead be based on minimizing foraging time and predation risk as indicated by Schroder (1979).

The unusual dietary preferences and caching behavior of kangaroo rats has the potential to make substantial contributions to the development of optimal foraging and food caching theories. Further investigation of this system will thus undoubtedly provide considerable insight into optimal behavior.

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Table 1. Mean moisture content ($\pm$ SE) of seed treatments at the start and end of the seed preference experiments

Experiment number	Days imbibed	Initial moisture content (%)	Initial[a] grouping	Final moisture content (%)	Final[a] grouping
1	D[b]	3.68 ± 0.05	a	4.74 ± 0.16	a
	0	6.28 ± 0.03	b	8.03 ± 0.11	b
2	1	20.66 ± 0.28	a	5.63 ± 0.11	a
	2	23.42 ± 0.45	b	6.19 ± 0.20	a
	3	24.48 ± 0.24	c	5.79 ± 0.25	a
3	1	16.36 ± 0.32	a	3.64 ± 0.04	a
	2	18.51 ± 0.22	b	4.19 ± 0.12	b
4	D[b]	2.56 ± 0.01	a	5.53 ± 0.41	a
	0	6.79 ± 0.09	b	9.22 ± 0.23	b
5	1	12.59 ± 0.17	a	2.73 ± 0.06	a
	2	18.49 ± 0.34	b	5.02 ± 0.06	b
	3	25.75 ± 0.23	c	6.15 ± 0.26	c
6	1	15.17 ± 0.06	a	3.31 ± 0.06	a
	2	18.60 ± 0.13	b	4.95 ± 0.80	b

[a] Grouping within an experiment, means with the same letter are statisically equivalent at the $P = 0.05$ level. For each initial moisture content $N = 5$, $N = 3$ for each final moisture content

[b] D = dried seeds

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Table 2. Mean nutritional composition (± SE) of both the non-imbibed and 3-day imbibed barley seeds analyzed

| Days imbibed | % dry mass | | | | | Moisture content (% wet mass) | Energy content (kJ/g) |
	Protein	Lipid	Carbohydrate	Ash	Digestibility		
0	9.51 ± 0.23	2.00 ± 0.49	81.53 ± 0.98	2.77 ± 0.53	94.77 ± 0.90	9.37 ± 0.15	17.91 ± 0.14
3	9.49 ± 0.10	1.58 ± 0.09	81.26 ± 0.77	2.49 ± 0.31	94.47 ± 0.53	27.84 ± 0.62	18.08 ± 0.06

Fig. 1. Mean body mass of kangaroo rats on the non-imbibed (solid line) and the 1-day, 12 h-dried (dotted line) seed diets. The abscissa indicates number of days on the diet. The ordinate is mean rodent body mass.
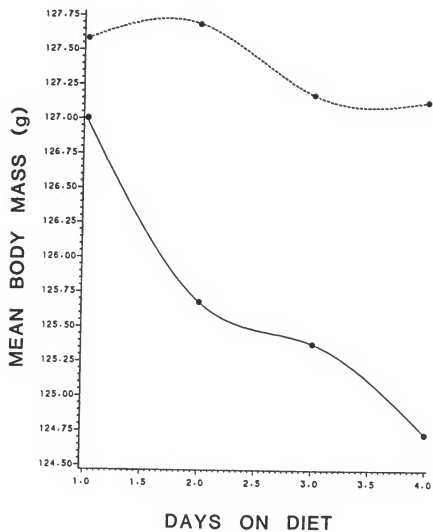
Fig. 2A-F. Histograms indicating the mean (± SE) amount of seeds for each treatment ingested in the seed preference experiments. The abscissa indicates seed treatments which are dried (D) or the number of days imbibed. The ordinate is the mean intake per subject, in grams. Those bars within an experiment sharing a common lower-case letter are statistically equivalent at the P = 0.05 level.
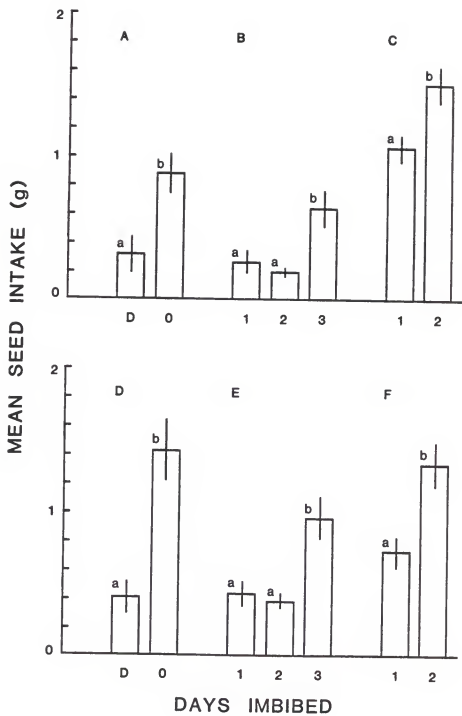
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THE EFFECTS OF MOISTURE CONTENT AND METABOLIC WATER PRODUCTION
ON DESERT RODENT SEED PREFERENCES

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AN ABSTRACT OF A MASTER'S THESIS

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Kangaroo rats (family Heteromyidae) are mainly granivores. These desert rodents do not drink water, they instead depend upon preformed water in their diet and the metabolic water produced by food oxidation. The oxidation of different nutrients produces different amounts of metabolic water. At low humidities, oxidizing carbohydrates produces a net metabolic water gain, whereas lipid metabolism results in a net water loss. Protein metabolism produces a severe water loss. Under humid conditions, carbohydrate metabolism again produces a net metabolic water gain, and protein metabolism still results in a large water loss. Lipid oxidation at high humidities, however, produces a net metabolic water gain. Because the catoblism of some nutrients found in seeds produces a net water loss, the seeds consumed must also contain some preformed water for the rodents to maintain a positive water balance.

Diet preference experiments involving semi-synthetic diets were performed to determine the influence of net metabolic water production on the seed preferences of <u>Dipodomys spectabilis</u>, and seeds imbibed to different moisture contents were used to assess the effects of water content on the diet choice of these rodents. Results indicate that kangaroo rats usually prefer diets that produce the greatest net metabolic water gain, regardless of energy content. The results also demonstrate that these rodents always prefer the moistest seeds available and they respond to very small differences in water content. Kangaroo rats thus maximize overall water intake through their seed choice.