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Effects of Food Deprivation and Metabolic Fuel Utilization on Food Hoarding by Jirds (*Meriones shawi*)

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DEMAS, G. E. AND T. J. BARTNESS. *Effects of food deprivation and metabolic fuel utilization on food hoarding by jirds* (Meriones shawi). PHYSIOL BEHAV **67**(2) 243–248, 1999.—Food hoarding plays an important role in the energetic repertoire of a variety of mammalian species. Both food hoarding and food intake have been examined in rodents using several energetic challenges including food deprivation, treatment with metabolic fuel blockers, and enhancement of fuel storage. In the present experiment, we examined food hoarding by female jirds (*Meriones shawi*), a desert rodent species occupying the arid steppes and desert regions of Egypt. Jirds are prodigious hoarders in the field; however, virtually nothing is known about their hoarding within controlled laboratory settings. In the present study, the effects of food deprivation as well as alterations in metabolic fuel utilization (i.e., 2-deoxy-D-glucose and isophane insulin) on food hoarding and food intake were tested in female jirds using a simulated burrow system. Jirds decreased body mass and increased food consumption following either 32 or 56-h food deprivation. Food hoarding, however, was virtually abolished after food deprivation and treatment with 2-DG. In contrast, isophane insulin treatment had no effect on food consumption or hoarding in this species. Taken together, the present results suggest that total body mass (fat), rather than short-term metabolic fuel utilization, regulates both food consumption and hoarding in female jirds. In addition, these results provide a novel set of appetitive responses to these energetic challenges in small mammals. © 1999 Elsevier Science Inc.

Energetics Desert rodents Metabolic fuels Food intake 2-DG Insulin

ANIMALS require a balanced energy budget (i.e., energy intake must be equal or greater than energy expended) in order to survive and reproduce. To accomplish this goal, animals must maintain a relatively constant flow of energy input despite fluctuating energy supplies and demand (28). Energetic deficits can be overcome by small mammals through either decreases in energy expenditure (e.g., reducing metabolic rate) or increases in energy intake (e.g., increasing body fat stores). Another way by which energy demands can be met is through food hoarding. During times of high food availability, food can be collected and stored externally in the form of a cache; this cache can be consumed later during times of food scarcity (7,26,27).

A wide range of rodent species exhibit food hoarding under both field and laboratory conditions. For example, food hoarding occurs among Mongolian gerbils (*Meriones unguiculatus*), laboratory rats (*Rattus norvegicus*), white-footed mice (*Peromyscus leucopus*), deer mice (*Peromyscus maniculatus*), as well as both Syrian (*Mesocricetus auratus*) and Siberian (*Phodopus sungorus*) hamsters [reviewed in (27)]. Despite the ubiquity of food hoarding, very little is known regarding the underlying physiological mechanisms controlling food hoarding. As for food intake, however, the onset and offset of food hoarding is assumed to be "regulated"(17). For example, conditions that reduce body mass (primarily in the form of a loss of body fat) increase food hoarding in several species (2,8). Both food deprivation and chronic food restriction increases food hoarding in laboratory rats (8), and Syrian (25,29), and Siberian hamsters (2). Beyond these relatively superficial relations, the mechanisms underlying food hoarding are largely unknown in any species.

Despite considerable data on food hoarding in commonly studied laboratory species, such as rats and hamsters, very little is known about hoarding in other less domesticated spe-

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cies. For example, several species of jirds within the genus *Meriones* (also commonly known as Mongolian gerbils) have been reported to hoard extensively in the field. Jirds are desert rodents that inhabit clay and sandy deserts, arid steppes, grasslands, and mountain valleys ranging from Mongolia to Egypt (15). Jirds are terrestrial rodents that spend most of their time occupying underground burrows that contain several small chambers used for food storage (15). They are believed to remain underground for long periods in the winter, living off of food hoards consisting mainly of seeds, green plants, and insects (14). Few studies have examined food hoarding by jirds within the laboratory. For example, in *M. unguiculatus*, food hoarding is extremely low in both males and females when fed ad lib in the laboratory (11, 16,17). Food hoarding, however, increases considerably after 1–2 weeks of food restriction in this species (17), and is greater in females than males (16). The discrepancy between field data indicating extensive hoarding by *M. unguiculatus* and laboratory studies reporting low hoarding in ad lib-fed jirds may be due to differences in food availability. That is, hoarding may be minimal when food is abundant and maximal when food is relatively scarce. Taken together, these results suggest that, as for rats and hamsters, food hoarding is regulated by food (energy) availability within the genus *Meriones*.

Food hoarding by *M. shawi*, a species inhabiting the desert regions of Egypt and Morocco, has not been studied in the laboratory. Therefore, the goals of the present study were to address the following questions: 1) do jirds (*Meriones shawi*) hoard food in an ecologically relevant laboratory setting, 2) does food deprivation affect food intake and food hoarding, and 3) does glucoprivation or enhanced storage of metabolic fuels affect food intake and hoarding by this species?

MATERIALS AND METHODS

Animals

Ten adult (10–12 months of age) female jirds (*Meriones shawi*), ranging from 114.34 to 165.49 g body mass, were wild trapped and obtained from a commercial supplier (El-Hakim, Egypt). All animals were group housed (two to three per cage) in polypropylene cages in a colony room illuminated with a 24-h L:D (14:10) light cycle (lights on 0400 h EST). Temperature was kept constant at 20 ± 2°C. Food (Purina Rodent chow #5001) and tap water were available ad lib until the start of the experiment. Two weeks before the start of the experiment, animals were housed individually and provided 75 g of food pellets (Formula A, P. J. Noyes, Lancaster, NH) in place of the standard chow. All procedures were approved by the Georgia State University Institutional Animal Care and Use Committee PHS guidelines and were in accordance with CDC guidelines for housing and handling wild animals.

Experimental Procedure

At the start of the experiment, animals were housed in a special hoarding apparatus, based on the design of a smaller version of the apparatus (2), consisting of two polypropylene cages (45 × 25 × 20 cm) connected by polyvinyl chloride (PVC) tubing (7.5-cm i.d.). The floor of the lower cage (i.e., the simulated burrow) was covered with 2–3 cm of absorbent bedding material (Alphadry Bedding, Shepard Specialty Products, Kalamazoo, MI) along with two 5 cm^2 cotton nestlets (Ancare, Manhasset, NY). The water bottle was placed on the top of the burrow cage. Food pellets (50 g) were available in a plastic Petri dish in the top cage. The caging system was designed to simulate natural hoarding by: 1) separating the food source from the burrow by both distance and time, and 2) requiring some effort to obtain food.

Animals were given ad lib access to the food pellets initially; however, the degree of hoarding was consistently low among all animals. Previously, we showed that food hoarding can be increased in nocturnal animals by restricting food availability to the center of the dark portion of the LD cycle (i.e., when the animals are active) (2). Thus, after 2 weeks of ad lib access to pellets, food was provided 1 h before lights out. The remaining food was removed 4 h after lights on and food intake and hoarded food were measured, and the animals were weighed. The amount of food hoarded was operationally defined as food found in the lower cage or in the tube immediately outside the cage. Food intake was defined as the initial weight of the pellets (e.g., 50 g) minus the remaining food in the top cage and hoarded food. All measures were determined to the nearest 0.1 g. A fresh allocation of pellets was returned to the top cage 1 h before lights out. Baseline assessment was conducted for 2 weeks to achieve stable levels of body mass, food intake, and food hoarding by all animals.

Food Deprivation

Jirds were food deprived to determine the effects of food deprivation on food hoarding. After baseline, hoarding was determined, animals were quasi-randomly divided in two groups. The first group of animals ($n = 5$) were food deprived for 32 h, while the remaining animals were food deprived for 56 h. These two fast lengths have been used previously to successfully increase food hoarding levels by Siberian hamsters (2,29). Experimental groups were matched according to body mass and hoard size as best as possible. Food deprivation began in the morning at the time that remaining food was normally removed, and refeeding occurred (i.e., 1 h before lights out, when food was normally returned to the animals during baseline testing) either 32 or 56 h after food deprivation. Body mass was measured daily during food deprivation. At the end of food deprivation, animals were refed according to the protocol established during the food-restricted baseline (i.e., food was restricted to the dark portion of the photoperiod). Body mass, food intake, and hoard size were determined daily for 1 week after refeeding as above.

2-DG–Induced Glucoprivation

Animals were allowed to return to their previous baseline levels of body weight and food intake for 2 weeks following the food-deprivation tests. Next, the effects of blocking glucose utilization on food intake and food hoarding was tested using 2 deoxy-D-glucose (2-DG; Sigma, St. Louis, MO). Animals ($n = 10$) were then injected with 0.2 cc of 2-DG (750 mg/kg) sc. The dose of 2-DG was equal to that which induces hyperphagia in rats (23). Injections were given before the normal presentation of food in late afternoon across 2 successive days. Body mass, food intake, and hoard size were determined as above.

Insulin-Induced Enhancement of Energy Storage

Animals were allowed to return to baseline levels of food intake and hoarding for 2 weeks. Then, the animals were injected with long-lasting insulin (i.e., isophane insulin; Eli Lilly, Indianapolis, IN) to determine the effects of enhanced metabolic fuel storage on food intake and hoarding. Daily injections of isophane insulin dissolved in 0.9% saline were

given for 9 days sc according to the following injection schedule: Day 1: 0.625 U/kg, Day 2: 1.25 U/kg, Day 3; 2.5 U/kg, Days 4–7: 5.0 U/kg, and Days 8–9: 10 U/kg. Gradually increasing doses of insulin were given in an attempt to avoid severe insulin-induced hypoglycemia that could result in the death of these valuable animals. Injections of isophane insulin were given immediately before the presentation of food in late afternoon, as was done for 2-DG administration. Body mass, food intake, and hoarding was measured daily as above.

Statistical Analyses

Body mass, food intake, and hoard size were determined using a two-way (experimental group × day) mixed model analysis of variance (ANOVA) with repeated-measures design using a statistical computer software package (Sigma Stat, Jandel Scientific, San Rafael, CA). All post hoc comparisons of pairwise means were conducted using Tukey HSD tests. Differences were considered statistically significant if $p < 0.05$. Exact probabilities and test values are not presented to simplify and clarify the presentation of the results.

RESULTS

Food Deprivation

Jirds ate more after fasts of either 32 or 56 h compared with their respective baseline food intakes ($p < 0.05$; Fig. 1a); the elevated postfast food intakes were not different from one another. Food hoarding was completely eliminated in food-deprived jirds compared with prefast baseline levels ($p < 0.05$; Fig. 1b). There was a trend towards reduced body mass by jirds that were food restricted for either 32 or 56 h; however, this effect was not statistically significant (Fig. 1c).

2-DG and Isophane Insulin Treatment

Glucoprivation tended to reduce food intake in jirds; however, this effect was not statistically significant (Fig. 2a). Food hoarding was virtually eliminated by 2-DG treatment compared with baseline levels ($p < 0.05$; Fig. 2b). Body mass was unaffected by 2-DG treatment (Fig. 2c). Isophane insulin treatment did not affect on food intake, food hoarding, or body mass, regardless of the hormone dose used (Fig. 3).

DISCUSSION

The results of the present study demonstrate a novel set of appetitive responses in female jirds (*Meriones shawi*) to three energetic challenges: food deprivation, glucoprivation (2-DG treatment), and enhanced metabolic fuel storage (insulin treatment). Specifically, jirds stopped hoarding food after food deprivation and glucoprivation, and maintained basal food hoarding levels after increased metabolic fuel storage. In addition, jirds showed a postfast hyperphagia, but did not alter their food intake after either glucoprivation or enhanced fuel storage. The failure of fasts to increase food hoarding contrasts with the ability of food deprivation to increase food hoarding in laboratory rats and Siberian hamsters and, most importantly, in a closely related jirds species, *M. unguiculatus*. The differences in food hoarding responses between *M. shawi* and *M. unguiculatus* are not readily apparent, but may represent species differences in energy allocation strategies or differences in the methods used to measure food hoarding.

Jirds, like laboratory rats (1,12), house mice, and deer mice (20,23,24), increased food intake after food deprivation in the present experiment. These results are in contrast with those found for both Siberian (2) and Syrian hamsters (5,6,22) that do not increase food intake after a fast. The increase in food intake after a fast in the present experiment does not appear to be due to food deprivation per se, but rather is a consequence of food restriction. Specifically, the loss of body fat

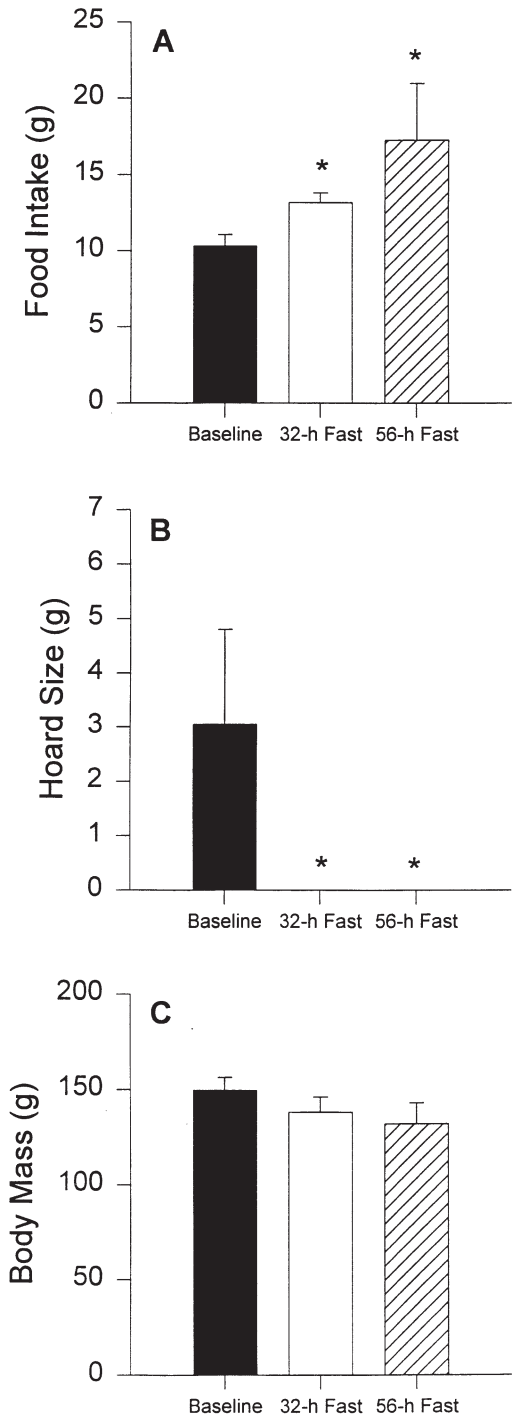

FIG. 1. Mean (±SEM) food intake (**A**), food hoarded (**B**), and body mass (**C**) in adult female jirds following baseline conditions or following 32- or 56-h fasts. Significant differences between group means ($p < 0.05$) are indicated by an asterisk (*).

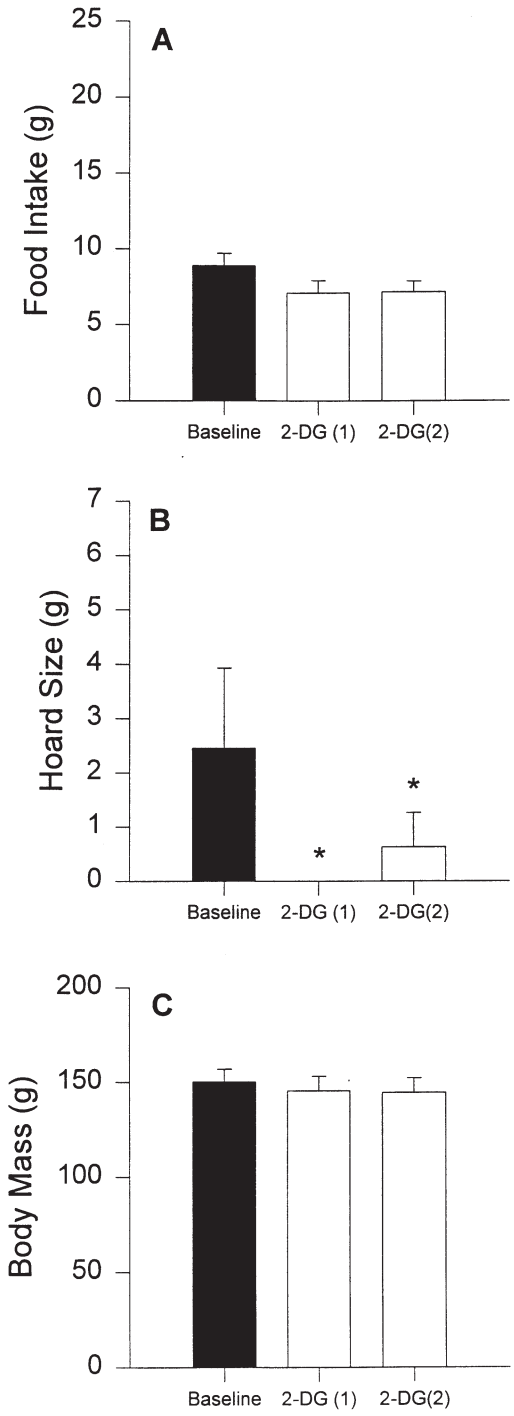

FIG. 2. Mean (±SEM) food intake (**A**), food hoarded (**B**), and body mass (**C**) in jirds following baseline conditions or after 1 or 2 days of treatment with 2-DG. All symbols and statistical conventions are as in Fig. 1.

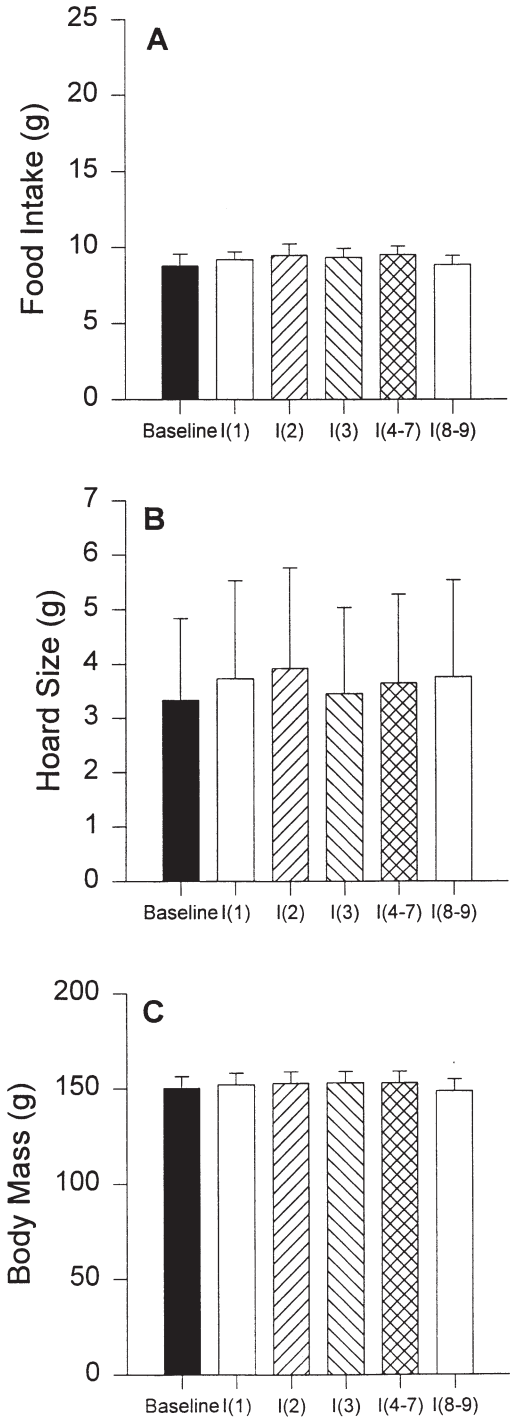

FIG. 3. Mean (±SEM) food intake (**A**), food hoarded (**B**), and body mass (**C**) in jirds following baseline conditions or after increasing doses of long-lasting insulin (isophane insulin). All symbols and statistical conventions are as in Fig. 1.

after prolonged food deprivation most likely triggers increased food intake by jirds. For example, in laboratory species such as rats, increased feeding and hoarding occurs only after several days of food restriction (13). These increases presumably occur at a time when energy intake is insufficient to maintain body mass, resulting in a loss of body fat. Similarly, female jirds did not increase food intake after treatment with the metabolic fuel utilization blockers 2-DG or long-lasting insulin. These results are consistent with those of deer mice that increase food hoarding after food deprivation, but

not after administration of 2-DG (24). Laboratory rats and house mice, however, increase food intake after treatment with 2-DG. The present results suggest that food intake and food hoarding in *Meriones* are more responsive to long-term changes in energy availability (e.g., total body fat) than short-term shifts in metabolic fuel availability. Conditions that limit energy availability transiently without affecting total body lipid stores (e.g., 2-DG, insulin) do not stimulate increased food intake by jirds or by Siberian hamsters (2). Although body fat levels were not determined in the present study, neither 2-DG nor insulin affected body mass. Because changes in body mass are due primarily to changes in body fat in adult mammals (28), it is likely that body fat remained unaffected by drug treatment in the present study. Food hoarding, unlike food intake, was virtually eliminated by food deprivation in the present experiment. These results are in marked contrast to the increased food hoarding seen in Syrian and Siberian hamsters, as well as rats, after fasting (2,8,30).

Administration of the glucose inhibitor 2-DG virtually eliminated food hoarding, but had no effect on food intake by jirds. These results are in marked contrast with the increases in food intake seen by laboratory rats after treatment with 2-DG (9,10,23), but in common with both Syrian (19,21–23) and Siberian (2) hamsters. The effects of 2-DG on food hoarding by laboratory rats and house mice remain untested. Food intake also was unaffected by long-lasting insulin treatment, similar to Siberian hamsters (3,4). In contrast, laboratory rats (18), and to a lesser degree Syrian hamsters (19,21) increase food intake after chronic administration of a long-lasting insulin. Food hoarding, as with food intake, was unaffected by long-lasting insulin treatment in jirds in the present study. This result suggests that energy allocation is not regulated by short-term changes in metabolic fuel availability in jirds. An alternative hypothesis is that neither 2-DG nor insulin were sufficient to alter glucose utilization at the doses used in the present study. Although glucose utilization was not assayed in the present study because of the limited supply of these animals and the unknown responses of these animals to serial bleedings, this possibility is unlikely, in that both 2-DG and isophane insulin alter blood glucose concentrations in every rodent species examined.

The primary finding of the present study is the virtual elimination of hoarding in jirds following either food deprivation or 2-DG treatment. The complete inhibition of food hoarding by food deprivation is directly opposite that which has been observed among laboratory rats (1,8,12,13), Syrian (11,30) and Siberian hamsters (2,29), and Mongolian gerbils (16). The reason for the cessation of hoarding after food deprivation is unknown; however, it is likely due to a reallocation of energy utilization in this species. In the presence of abundant food, jirds can consume the food and utilize it as energy or store it as fat. Alternatively, they can hoard food externally for future consumption. When food is relatively plentiful, jirds appear to store much of the available food in the form of an external hoard. In the presence of extreme energetic restrictions (i.e., food deprivation), however, jirds may shift their energy allocation such that most or all available energy is consumed rather than allocated to external energy storage (i.e., food hoard). The present results are consistent with idea that food hoarding is reduced or eliminated during times of extreme food shortage.

Taken together, the results of the present experiment suggest that food hoarding is curtailed in jirds in response to reduced food availability. Rather, jirds increase food consumption when possible to compensate for previous reductions in energy intake. In addition, these changes in energy allocation appear to be regulated by shifts in long-term energy stores (body fat), rather than short term changes in metabolic fuel utilization.

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