Published in final edited form as:

Physiol Behav. 2014 March 29; 127: 8–12. doi:10.1016/j.physbeh.2013.12.008.

Dynamic Modification of Hoarding in Response to Hoard Size Manipulation¹

John T. Garretson^{2,4} and Timothy J. Bartness^{2,3,4}

²Neuroscience Institute, Georgia State University, 24 Peachtree Center Ave NE, Atlanta, GA 30302-4010, USA

³Department of Biology, Georgia State University, 24 Peachtree Center Ave NE, Atlanta, GA 30302-4010, USA

⁴Obesity Reversal Center, Georgia State University, 24 Peachtree Center Ave NE, Atlanta, GA 30302-4010, USA

Abstract

Food hoarding is an evolutionary adaptation whereby animals store food for later consumption when food is limited or when predation risk while foraging is high. It also occurs as part of normal appetitive behavior by humans and non-human animals when they are hungry. Contrary to popular belief, humans do not overeat after food restriction/fasting, rather they increase food hoarding, as do hamster species, but not in laboratory rats or mice. Thus, this aspect of human appetitive behavior is better modeled by hamsters than laboratory rats and mice. Here we tested whether male Siberian hamsters (*Phodopus sungorus*) modify their daily food hoard size under ad libitum-feeding and after food deprivation when we artificially increased or removed their food hoard. When the food hoard was completely removed, hamsters hoarded more food the next day than did animals where the hoard was surreptitiously increased. Hamsters that had alternating daily hoard increases/decreases rapidly adjusted their food hoarding inversely proportional to food hoard size. Similarly, after 48 h of food deprivation, a stimulus that initiates high levels of food hoarding upon refeeding in this species, hamsters with artificially increased food hoard size hoarded significantly less than did hamsters where we left the hoard unaltered additionally suggesting that food hoard size directly affects food hoarding. Collectively, as we previously found when the caloric value of the food offered was increased or decreased, food hoard size is in some sense 'regulated' and not simply a reflexive response triggered by intermeal hunger or food deprivation.

Keywords

Siberian hamster; food deprivation; hunger; fasting

© 2013 Elsevier Inc. All rights reserved.

¹Address all correspondence to: Dr. Timothy J. Bartness, Department of Biology, 24 Peachtree Ctr Ave NE, Atlanta, GA, 30302-4010, bartness@gsu.edu, Office Phone: 404 413-5334, FAX: 404 413-5301.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

1 Introduction

Food hoarding is achieved when animals forage for and store food for later consumption. Food hoarding is an appetitive ingestive behavior expressed across most animal species (for review see: [1]) including humans. Restricted food access, food deprivation/fasting and to a lesser extent the hunger that occurs between meals are the strongest stimuli that trigger food hoarding (for review see: [2]). Contrary to popular belief, humans exhibit essentially no or little post fast/food restriction-induced increases in eating (for review see: [2]). Rather, hungry humans 'overhoard' by bringing home more food even after mild periods of no food versus their fed counterparts [3–5]. Similarly, various hamster species including Siberian hamsters (*Phodopus sungorus*) studied here, markedly increase their food hoarding, but not food intake, with refeeding after food deprivation [6–9]. Thus, this appetitive ingestive behavior of food hoarding is more similar than different between humans and Siberian hamsters. Therefore, studies of food hoarding by Siberian hamsters appear to be an appropriate model for the study of the environmental and physiological controls of this appetitive ingestive behavior in humans (for review see: [2]).

We have identified several hormones and neuropeptides that are affected by food deprivation naturally such as ghrelin, agouti-related protein and neuropeptide Y and when given exogenously mimic in duration and magnitude the food deprivation-induced increases in food hoarding [10–12], but are not fully explored or understood. Of the many questions remaining to answer, one that transcends both the environmental and physiological factors governing food hoarding is whether food hoard size is in some sense 'regulated'. That is, are there processes engaged when food hoarding is triggered that ultimately result in the maintenance of a relatively constant food hoard size, whether it is the physical size of the hoard (*e.g.*, number of hoarded objects) or the overall caloric value of the hoard? We previously partially addressed this issue by challenging *ad libitum*-fed Siberian hamsters with food sources of varying caloric density relative to their standard chow-like food pellets [13]. Specifically, when caloric density was decreased by the addition of a cellulose diluent in the pellets, the number of food pellets hoarded increased proportionately to the decrease in caloric density such that the overall caloric value of the food was maintained, a feat accomplished within the first 24 h of the diet switch. Complementary to this, when the caloric density of the food was increased by adding dietary fat to the pellet composition, the number of food pellets was proportionately decreased such that overall caloric density was maintained – again accomplished within the first 24 h of the diet switch [13].

Collectively, the above data suggest caloric maintenance of food hoard size in *ad libitum*-fed hamsters. Untested, however, was whether food hoard size would be stable if food from the burrow was surreptitiously added or subtracted rather than altering caloric content or diet type thereby increasing or decrease the size/caloric value of the food hoard. In addition, would any attempt to keep food hoard size constant be affected by food deprivation, the stimulus that most robustly naturally increases food hoarding? Another way of thinking about the possible maintenance of food hoard size tested here is whether the underlying mechanisms involved in daily food hoarding under *ad libitum* feeding conditions or following food deprivation trigger an inflexible almost 'fixed action pattern-like' amount of food hoarding or whether the hoarding is flexible responding to some characteristic of the food already cached. In nature, decreases in food hoard size could occur with food pilfering by conspecifics or heterospecifics and increases could occur via additions made by their pair-bonded mates or offspring as they communally burrow [14]. To accomplish this, we added or subtracted food from their hoard to test whether appropriate compensation occurred (decreased or increased food hoarding, respectively). We also challenged the hamsters with food deprivation to test their ability to adjust hoard size with surreptitious additions and subtractions from their food hoard.

2 Method

2.1 Animals

Three month old male Siberian hamsters ($n = 40$) from our breeding colony raised in a long photoperiod (16:8 light:dark cycle; lights on at 19:00) were weaned at 18 d of age. Lineage of our breeding colony has been described previously [15]. Hamsters were assigned to individual polypropylene cages ($456 \times 234 \times 200$ mm) containing Alpha-Dri bedding (Specialty Papers, Kalamazoo, MI), one cotton Nestlet (Anacare, Belmore, NY) with both tap water and the test diet (Dustless Precision Pellets, Purified 75 mg pellets; Bio-Serv, Frenchtown, NJ) available *ad libitum*. Animals were then acclimated to a reverse 16:8 cycle light:dark cycle (lights on at 21:00) for 14 d before manipulations began to make data collection more convenient for the experimenters. We then assigned animals to experimental groups based on body mass and percent change in body mass over the 14 d diet and photoperiod acclimation. All procedures were approved by the Georgia State University Institutional Animal Care and Use Committee and were in accordance with Public Health Service and United States Department of Agriculture guidelines.

2.2 Materials and Procedure

2.2.1 Foraging-Hoarding Apparatus—After the 14 d photoperiod acclimation, we transferred the hamsters to our simulated burrow caging system where foraging, hoarding, and food intake was quantified daily (see [16] for detailed description of this apparatus). In brief, two cages were connected by a convoluted tunnel of polyvinyl chloride tubing (38.1 mm inner diameter and ~1.52 m in length) with the clear top cage ($456 \times 234 \times 200$ mm; 'foraging cage') containing tap water available *ad libitum*, a running wheel (584 mm diameter), and a hole through which food pellets can be dispensed [food pellet dispenser (Med Associates, Georgia, VT)] when earned (described below). The opaque covered bottom cage ($290 \times 180 \times 130$ mm, 'burrow cage') contained Alpha Dri-bedding and one cotton nestlet. A computer running MEDPC-IV software (Med Associates Inc., Georgia, VT) was connected to both the running wheel and food pellet dispenser of each simulated-burrow cage which recorded wheel revolutions and systematically triggered the food dispenser to deliver one food pellet into the foraging cage for every 10 wheel revolutions during the entire duration of the study across all animal treatment conditions, unless stated otherwise below. Each hamster was assigned to an individual simulated-burrow system, given constant access to their running wheel, and allowed to freely roam between the foraging and burrow cages through the convoluted PVC tubing. Note that Siberian hamsters earn pellets and hoard them in the burrow cage reliably and without training [16].

We defined food pellets stored in both the burrow cage and in hamster cheek pouches as hoarded food. Food pellets recovered from the foraging cage that were neither eaten nor hoarded were defined as surplus pellets, but these were always insignificant. Food pellets earned (wheel revolutions divided by 10) were defined as 'pellets foraged' and 'food intake' was defined as the pellets foraged minus all pellets recovered. All food pellets and partial pellets were recovered 4 h prior to lights off. Food was assessed at this time because Siberian hamsters hoard food primarily at night and eat from the hoard during the day; therefore, collecting the food at this time assures that we are measuring at least the vast majority of their hoarded food (C. Klein and T. J. Bartness, unpublished observations). Food amounts were measured with a precision balance set to 'parts' measurement, resulting in one 75 mg food pellet = 1 with fractions of pellets computed by the balance. Surplus pellets and pellets hoarded were collected, weighed, and food intake calculated daily for all hamsters. All recovered pellets were discarded daily.

3 Experiment 1

3.1 Experimental groups

To assess the potential of Siberian hamsters to adjust their food hoarding based on food hoard size, we manipulated their hoard in three different daily conditions: 1) hoard was either removed, weighed, and discarded – the so-called ‘*removed group*’ ($n = 10$), 2) removed, weighed, discarded and replaced with the same number of fresh pellets – the so-called ‘*replaced group*’ ($n = 10$), a control for any disruption caused by food removal, 3) or removed, weighed, discarded then replaced with a fixed value of 100 fresh pellets – the so-called ‘*enhanced*’ group ($n = 10$). To test if animals adjusted their hoarding acutely and in dynamic conditions, a fourth group of separate hamsters alternated between *removed*, *replaced*, and *enhanced* for two days each over a six day period ‘*alternated*’ ($n = 10$). All food replacements were discreetly placed in a corner of the vacant burrow cage while the hamster was out of view in either the convoluted tubing connecting the burrow to the foraging cage, or in the foraging cage. All animals had continual access to all portions of their caging system, including the ability to earn food based on wheel revolutions, throughout Experiment 1.

3.2 Data Analysis

Food hoarding, food intake and wheel running data were analyzed with one-way ANOVA. If hamsters hoard food based on the size of the food hoard, then *alternating* group animals would be expected to hoard differently with each alternation and thus their variability across the initial 6 d, during which their hoard size was first removed, then replaced, then enhanced, would be high relative to variability in any of the steady state groups. Therefore, average variance was compared between treatment groups that received either a fixed number (0 or 100) or alternating numbers of food pellets using Student’s *t*-test. In addition, within-subjects differences for the *alternating* group hamsters were assessed using repeated measures ANOVA to further identify if hoard size affected food hoarded when hoard size conditions varied every 2 d. All analyses were done using SPSS (version 20, Armonk, NY). Exact probabilities and test values were omitted for simplicity and clarity of presentation. Statistical significance was considered if $p < 0.05$ unless otherwise noted.

3.3 Results and Discussion

Hoard size manipulation directly affected hoarding overall (Figure 1A; $p < 0.05$). Hamsters in the *enhanced* group hoarded significantly less than did those in the *removed*, *replaced*, or *alternated* groups ($p < 0.05$). Hamsters that received a different hoard condition every two days (*alternated* group) hoarded differentially with each condition increasing and decreasing hoard size with removal and addition of food, respectively, expressed as variability across the 6 d period, than did hamsters in fixed pellet conditions (*removed* group collapsed with *enhanced* group; Figure 1B; $p < 0.05$). Hoard size acutely affected *alternated* group animals because each hoarding condition spurred a within-subject level of food hoarding such that *enhanced*, *replaced* and *removed* conditions triggered low, medium and high levels of food hoarding, respectively $p < 0.05$. Neither wheel revolutions nor food intake were different between the treatment groups throughout the duration of Experiment 1.

The results of Experiment 1 suggest that Siberian hamsters hoard food based on the amount of food currently stored in their burrow. This infers that hamsters can, in some manner, ‘sense’ the amount of food stored in their burrows that, in turn, affected their subsequent behavior such that a small hoard size increased hoarding whereas a large hoard size decreased hoarding. Moreover, this ability may prepare hamsters for unpredictable changes in environmental or physiological factors that affect food hoarding (e.g., periods of food shortage, temperature changes, predatory risk, pilfering [17]) and is presumably relevant to

other hoarding species including humans. In humans, it is possible that a decrease in the normal surfeit of food stored in most homes of industrialized nations could trigger foraging (shopping) and hoarding (storage) of food independent of hunger, thereby further increasing readily available food to eat and perhaps increase the ease and likelihood of overeating [2]. The types of food (caloric density, composition) were not varied in this experiment, but in free-living humans, obese people tend to bring home more calorically-dense and fat-laden food than do their lean counterparts [18].

4 Experiment 2

4.1 Food deprivation

To test if the ability to adjust the size of the food hoard to experimenter-induced alterations in food hoard size occurs with food deprivation-induced increases in food hoarding, we food deprived the hamsters from Experiment 1 for 48 h, a food deprivation period previously shown to elicit marked increases in Siberian hamster food hoarding [2], but not food intake. Because in the laboratory, by contrast to the wild, these animals are ~50% body fat [e.g., [19, 20], a longer food deprivation period than normally acceptable for laboratory rats and mice is needed to stimulate food hoarding in hamsters ([6]). Therefore, we measured food hoard size of each of the *removed*, *replaced*, and *enhanced* groups across 3 d post-refeeding. To reduce the need for more hamsters in the spirit of the 3 R's of the Animal Welfare Act [21] the *alternated* group animals were assigned to either the *removed* ($n = 14$), *replaced* ($n = 13$), or *enhanced* ($n = 13$) groups and all groups were re-balanced for current body mass and then by percent change body mass throughout Experiment 1.

4.2 Post-habituation hoard switch

Finally, we tested whether long-term exposure to either the *removed* or the *enhanced* food hoard treatment affected the flexibility to respond appropriately to subsequent experimenter-induced changes in food hoard size. Food-deprived/refed hamsters were allowed to recover baseline hoarding levels for 14 d after refeeding in which they either had all pellets removed from or received 100 fresh pellets into their burrow cage daily. At that time, hamsters in the *removed* group were then switched to the *enhanced* group and *vice versa*.

4.3 Data Analysis

Food deprivation induced food hoarding, food intake and wheel running data were analyzed with one-way ANOVA followed by pre-planned comparisons between treatment groups (*removed*, *replaced*, and *enhanced*) with adjusted p values to reduce type I error as in Experiment 1. To assess whether habituation to either replace or enhance treatments prevented animals from adjusting their food hoarding acutely, within-subjects comparisons between pre and post-switch periods were made within each animal using paired-samples t.

4.4 Results and Discussion

Appropriate adjustments in food hoard size in the *replaced* and *enhanced* conditions were differentially affected by food deprivation when compared with pre-deprivation baseline hoarding levels (Figure 2A). That is, hamsters in *replaced* and *enhanced* conditions did not increase food hoard size to the same elevated extent above their pre-deprived average hoarding baseline as did hamsters where their food hoard was removed ($p < 0.05$). Specifically, hamsters in the *removed* condition hoarded more than animals in the *enhanced* condition 72 h post refeeding ($p < 0.05$) with suggestions of higher hoarding at 24 h ($p = 0.08$) and 48 h ($p = 0.09$) postrefeeding; however, they did not hoard more than hamsters in the *replaced* condition (Figure 2A). Furthermore, hamsters in the *enhanced* condition hoarded less 72 h post-refeeding compared with those of the *replaced* condition (Figure 2A; $p < 0.05$).

with a suggestive increase in hoarding 24 h post-refeeding ($p=0.06$). After the post-refeeding baseline hoarding levels were reached, hamsters in the *removed* condition were switched to the *enhanced* condition and *vice versa*; hamsters in the *removed* condition—despite the order of the switch—always hoarded more than hamsters in the *enhanced* condition (Figure 2B; $ps<0.05$).

Wheel revolutions were not different between treatment groups throughout the duration of these experiments. Cumulative food intake was not different between groups except that animals in the *enhanced* condition ate less than did all others at 24 h, 48 h, and 72 h post-refeeding (Figure 2C; $ps<0.05$).

Collectively, the data from Experiment 2 suggest that food deprivation affects Siberian hamster food hoarding differentially based on the amount of food in food hoard. That is, greater amounts of stored food reduce the ability of food deprivation to induce increased food hoarding. The relatively constant food intake typical of this and other hamster species under *ad libitum* food conditions and even after food deprivation-refeeding (for review see: [2, 22]) appears to be an adaptation to conserve food reserves after times of severe food availability and to stimulate food hoarding to rebuild external energy stores. Such energy adaptations may be beneficial to other food hoarding species including humans after times of energy shortage.

5 General Discussion

The data from these present experiments strongly suggest that the amount of food hoarded by Siberian hamsters depends upon the amount of currently stored food. That is, manipulating food hoard size affected subsequent hoarding by both increasing hoarding when food hoard size was artificially decreased and decreasing hoarding when food hoard size was artificially increased whether occurring under conditions of *ad libitum* food access or after food deprivation-refeeding conditions. These data support the notion that Siberian hamsters, and likely other hoarding species, dynamically control their hoarding based on unpredictable changes in their hoard size (*e.g.* pilferage, or additions by conspecifics in non-solitary species). As evidence of dynamic control, hamsters in the *alternated* group, where the size of the food cache was changed every 2 d, hoarded similar quantities of food to that of the three other groups (*removed*, *replaced*, and *enhanced*) on both days of each treatment condition, suggesting a rapid adjustment of food hoarding whether the hoard was added to, stayed the same or was subtracted from. Animals in either the *removed* or *enhanced* groups, which both received a fixed number of pellets, each hoarded a similar amount of pellets from day-to-day maintaining relatively low hoard variability across days; however, groups in which hoard size was alternated showed different daily amounts of hoarding depending on their current treatment condition—further characterizing the rapidity with which the amount of hoarding is based on the current cache size.

Food deprivation or restriction is one of the principal, if not the principal stimulator of food hoarding (for review see: [1, 2, 22]). In Siberian hamsters studied in the laboratory, 48 h of food deprivation robustly stimulates food hoarding (*e.g.*, [6]). Hamsters which had their food hoard size increased, however, did not increase their hoarding as markedly in response to food deprivation compared with hamster that had their entire hoards removed or replaced (no net change for the latter). This suggests that hamsters can in some manner ‘sense’ the size of their food hoard and that if it is increased, even artificially, this decreases future food hoarding even if this is occurring in the context of food deprivation-refeeding. Because wheel running was not different among all the groups that increased food hoarding with refeeding, this suggests that food hoard size may specifically affect food hoarding *per se*, rather than more generally increasing foraging and/or locomotor activity.

Hamsters that had the same hoard size treatment for 14 consecutive days and then were switched to the opposite condition (*i.e.*, *removed then enhanced*, or *enhanced then removed*) rapidly (within a day) altered their food hoarding appropriately to maintain a relatively constant food hoard size consistent with each condition. These data are yet another example that hamsters seem to continually adjust their food hoarding based on daily changes in their hoard size. Although it is easier to understand how Siberian hamsters could rapidly (within a day) adjust their food hoarding and food hoard size appropriately when the food source was calorically decreased or increased, as we had shown previously based on presumed post ingestive consequences of the new food eaten [13], it is more difficult to understand how Siberian hamsters also could rapidly (also within a day) adjust their food hoarding and food hoard size appropriately when the size of the food hoard was experimentally surreptitiously added to or subtracted from and the food source characteristics (*e.g.*, caloric density) were not changed. This could possibly be an evolutionary adaptation to resist spoilage as seen with Eastern wood rats (*Neotoma floridana*) that do not store perishable grapes but rather non-perishable acorns and seeds [1].

We acknowledge that the *enhanced* condition is not especially ethologically relevant except for species such as Siberian hamsters where the mate of a pair contributes some to the hoard [7], but this gross addition served to test if hamsters were somehow aware of the amount of food in their burrow independent of their food hoarding. Mechanisms of this hoard awareness are beyond the scope of this study; however, chemosensory, tactile, and visual cues likely play a role due to the involvement of these sensory systems during food acquisition in this species and others [1]. In the wild, collared pika (*Ochotona collaris*) have an apparent requisite amount of hay to hoard to make overwintering possible in most years suggesting assessment of hoard size can be critical for survival in highly-seasonal environments [23]

Collectively, these data demonstrate that Siberian hamsters alter their hoard size rapidly (within a day) in response to experimenter-induced increases or decreases in food hoard size and add to our previous data [13] showing alterations in food hoard size based on the caloric density of the food hoard. Therefore, Siberian hamsters have the capability to dynamically and rapidly control their food hoard size in a manner suggesting some sort of overall ‘regulation’ of this external energy source. Because acquisition (foraging) and storing (hoarding) of food is a precursor to food intake across many animal species [1], including humans (for review see: [2]), the importance of understanding the ability to control the amount of these external energy stores could provide mechanisms that could be targeted pharmacologically and/or behaviorally to limit the amount of calories and types of food conveniently located in the home for easy access that may be too tempting not to eat—whether for physiological or psychological needs. Thus, it is easy to envision how increases in externally stored calories could contribute to the surfeit of internally stored energy as body fat thereby promoting obesity. This emphasizes, therefore, the obvious – one cannot eat what one does not possess.

Acknowledgments

The authors thank Daniel Vizcaino, Danni Liu, and Dominiq Okoduwa for their help with daily data collection. We also thank Department of Animal Resources staff at Georgia State University for their research support expertise and excellent animal care. This research was supported by the National Institutes of Health R01 DK078358 to TJB.

Reference List

1. Vander Wall, SB. Food hoarding in animals. Chicago: Univ. Chicago Press; 1990.
2. Bartness TJ, Keen-Rhinehart E, Dailey MJ, Teubner BJ. Neural and hormonal control of food hoarding. *Am. J Physiol.* 2011; 301:R641–R655.

3. Dodd DK, Stalling RB, Bedell J. Grocery purchases as a function of obesity and assumed food deprivation. *Int. J. Obes.* 1977; 1:43–47. [PubMed: 617107]
4. Beneke WM, Davis CH. Relationship of hunger, use of a shopping list and obesity to food purchases. *Int. J. Obes.* 1985; 9:391–399. [PubMed: 3830932]
5. Mela DJ, Aaron JI, Gatenby SJ. Relationships of consumer characteristics and food deprivation to food purchasing behavior. *Physiol Behav.* 1996; 60:1331–1335. [PubMed: 8916190]
6. Bartness TJ, Clein MR. Effects of food deprivation and restriction, and metabolic blockers on food hoarding in Siberian hamsters. *Am. J. Physiol.* 1994; 266:R1111–R1117. [PubMed: 8184952]
7. Bartness TJ. Food hoarding is increased by pregnancy, lactation and food deprivation in Siberian hamsters. *Am. J. Physiol.* 1997; 272:R118–R125. [PubMed: 9038999]
8. Day DE, Bartness TJ. Fasting-induced increases in hoarding are dependent on the foraging effort level. *Physiol. Behav.* 2003; 78:655–668. [PubMed: 12782221]
9. Wood AD, Bartness TJ. Food deprivation-induced increases in hoarding by Siberian hamsters are not photoperiod-dependent. *Physiol Behav.* 1996; 60:1137–1145. [PubMed: 8884944]
10. Keen-Rhinehart E, Bartness TJ. Peripheral ghrelin injections stimulate food intake, foraging and food hoarding in Siberian hamsters. *Am. J. Physiol.* 2005; 288:R716–R722.
11. Boss-Williams KA, Bartness TJ. NPY stimulation of food intake in Siberian hamsters is not photoperiod dependent. *Physiol. Behav.* 1996; 59:157–164. [PubMed: 8848476]
12. Day DE, Bartness TJ. Agouti-related protein increases food hoarding, but not food intake by Siberian hamsters. *Am. J. Physiol.* 2004; 286:R38–R45.
13. Wood AD, Bartness TJ. Caloric density affects food hoarding and intake by Siberian hamsters. *Physiol Behav.* 1996; 59:897–903. [PubMed: 8778884]
14. Weiner J. Limits to energy budget and tactics in energy investments during reproduction in the Djungarian hamster (*Phodopus sungorus sungorus* Pallas 1770). *Symp. zool. Soc. Lond.* 1987; 57:167–187.
15. Bowers RR, Festuccia WTL, Song CK, Shi H, Migliorini RH, Bartness TJ. Sympathetic innervation of white adipose tissue and its regulation of fat cell number. *Am. J. Physiol.* 2004; 286:R1167–R1175.
16. Day DE, Mintz EM, Bartness TJ. Diet self-selection and food hoarding after food deprivation by Siberian hamsters. *Physiol. Behav.* 1999; 68:187–194. [PubMed: 10627080]
17. Whishaw IQ, Dringenberg HC. How does the rat (*Rattus norvegicus*) adjust food-carrying responses to the influences of distance, effort, predatory odor, food size, and food availability? *Psychobiology.* 1991; 19:251–261.
18. Ransley JK, Donnelly JK, Botham H, Khara TN, Greenwood DC, Cade JE. Use of supermarket receipts to estimate energy and fat content of food purchased by lean and overweight families. *Appetite.* 2003; 41:141–148. [PubMed: 14550311]
19. Bartness TJ, Hamilton JM, Wade GN, Goldman BD. Regional differences in fat pad responses to short days in Siberian hamsters. *Am. J. Physiol.* 1989; 257:R1533–R1540. [PubMed: 2604008]
20. Wade GN, Bartness TJ. Effects of photoperiod and gonadectomy on food intake, body weight and body composition in Siberian hamsters. *Am. J. Physiol.* 1984; 246:R26–R30. [PubMed: 6696099]
21. Animal Welfare Act. 2013
22. Keen-Rhinehart E, Dailey MJ, Bartness TJ. Physiological mechanisms for food-hoarding motivation in animals. *Philos. Trans. R. Soc. Lond B Biol. Sci.* 2010; 365:961–975. [PubMed: 20156819]
23. Morrison SF, Pelchat G, Donahue A, Hik DS. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. *Oecologia.* 2009; 159:107–116. [PubMed: 18987896]

Highlights

- Food hoard size rapidly affects hoarding
- Hoard is decreased or increased when surreptitiously enlarged or diminished
- Food deprivation does not increase hoarding for animals with enhanced food stores

A

Food Hoarding in Response to Hoard Size Changes

B

Hoarding Variability in Response to Hoard Size Changes

Figure 1.

A&B: Siberian hamsters hoard food based on hoard size. **A)** Mean +SEM difference in daily hoard size for groups in which food was either *removed*, *replaced*, or *enhanced* daily for six days each. Difference scores are produced by subtracting food present in hoarding cage from what was returned to their cage the previous day. **B)** Mean +SEM variance of food pellets hoarded comparing collapsed groups with variance in the *alternated* group (alternated between each hoard size treatment every two days). * = $p < 0.05$.

A

B

Changes in Food Hoarding With Alterations in Hoard Size

C

Food Intake in Response to 48 h Food Deprivation

Figure 2.

A–C. Sustained dynamic hoarding behavior after food deprivation and prolonged hoard conditions. **A)** Mean +SEM difference from baseline for animals in either *removed*, *replaced*, or *enhanced* conditions after food deprivation. **B)** Mean +SEM difference in daily hoard size before and after a switch from 12 days of either *removed* or *enhanced* to two days of *enhanced* or *removed*, respectively. * = $p < 0.05$. **C)** Mean +SEM cumulative number of food pellets eaten during 3 days post food deprivation among hoard size groups. *Enhanced* group ate significantly less than did *removed* or *enhanced* at all time periods. * = $p < 0.05$