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Abstract

It is important for animals to adapt to changes in food availability in order to survive. Hoarding is one method of accomplishing this and the golden hamster (Mesocricetus auratus) is particularly adept at hoarding. Previous literature suggests a connection between hoarding and stress. To further examine this connection, the present study looked at the effects of illumination and food deprivation on the hoarding behavior of male golden hamsters. The within-subjects design allowed each of the 12 subjects to be tested in each of the 4 conditions: 1) illumination and food deprivation, 2) illumination and no food deprivation, 3) food deprivation and no illumination, and 4) no illumination and no food deprivation. The results show 3 significant findings: 1) hamsters moved less food when food deprived than when not food deprived, 2) hamsters ate more food when food deprived than when not food deprived, and 3) there were fewer droppings in the foraging cage when illumination was present than when it was absent. These findings were opposite of those suggested by previous literature, thus providing more questions than answers about the hoarding behavior of the golden hamster.

Illumination and Food Deprivation as Determinants for Hoarding in Golden Hamsters

Animals in the wild must adapt to changing environmental conditions in order to survive. This follows directly from the theory of evolution by natural selection (Darwin, 1859). This adaptation may be morphological, physiological, or behavioral. In recent years, several sub-fields in biology and psychology have concentrated on behavioral adaptation. For example, sociobiology (Wilson, 1975), behavioral ecology (Krebs & Davies, 1978) and behavior systems theory (Timberlake, 1993) all examine the relationship between evolutionary adaptation and behavior.

Seasonal changes are one example of a situation in which adaptation is necessary. When seasons change, the availability of food often changes. As the weather changes animals must act accordingly, whether it is to consume or store extra food, migrate to another location, or alter their habitat (Morgan, 1947). Animals must also act to remain safe from predators (Weiten, 2001); this may mean feeding at specific times or simply staying hidden in the home area until the coast is clear. A third obstacle involves changes in food and water supply. Animals must be able to have access to (or have stored) these necessities in case of a shortage (Morgan, 1947).

Adaptations to the environment related to seasonal food availability are particularly critical because an organism will die in the absence of sufficient food or energy stores (Darwin, 1859). Changes in food supply are often the most detrimental to an animal's well being if the animal is not prepared to cope with a shortage. In natural and laboratory settings, animals experience temporary periods of limited food supply. These animals must exhibit certain biological adaptations in order to survive (Morgan, 1947). Evolution has produced several strategies for the survival of these animals.

One of the most common methods of survival involves the creation of body fat stores within the animal (Bartness & Wade, 1985). These fat stores allow the animals to go without food for a period of time and still function on the energy reserves in the stored fat. Many rodents show increases in food consumption prior to being food-deprived following previous food deprivation, which results in an increase in body fat; this is known as post-fast hyperphagia (Bartness & Wade, 1985; DiBattista & Bedard, 1987; Lea & Tarpy, 1986; Phillips, Robinson, & Davey, 1989; Rowland, 1982). This means that following a period of deprivation the animals will consume large quantities of food as soon as they are given access. Even animals such as the chicken, pig, and cow exhibit post-fast hyperphagia in response to inadequate access to food (Silverman & Zucker, 1976). If the animal were unable to have access to food for an extended period, then perhaps another method would be more appropriate.

Hibernation is another adaptation to food scarcity in which the animal reduces its motor activity and metabolism for a period, thus depleting energy normally provided by food intake at a slower rate (Berger & Phillips, 1995). As described by Bartness and Wade (1985), certain rodents such as ground squirrels, marmots, and woodchucks are known to hibernate during the winter. These animals, however, show an increased body weight, mostly as body fat, during an autumn pre-winter fattening phase. Then during the hibernation period, the fat stores are depleted, but the animals are still able to maintain a healthy body weight. Certain animals, however, do not store body fat and would thus require a different means of food storage, such as hoarding.

Hoarding is a behavioral adaptation that involves leaving the home area, finding a source of food, transporting the food back to the home area (or another secure location), and then burying the food (Jones & Pinel, 1990). This method allows the animal to eat normally without leaving the home area and without depending on internal fat reserves for energy (Phillips, Robinson, & Davey, 1989). This method is sometimes used in conjunction with winter hibernation.

These methods of biological adaptation are useful in varying degrees for different animals. Most rodents are capable of all three methods (Bartness & Wade, 1985; Phillips, Robinson, & Davey, 1989). Golden (Syrian) hamsters seem to be an exception. For example, Simek (1975) found that the golden hamster, unlike other mammals, shows a decline of percentage body fat in both winter and summer when exposed to intermittent starvation. Body fat stores are thus not a likely survival method for the Syrian hamster because they are not biologically predisposed to store fat. If the Syrian hamster is not storing fat on its body, perhaps it is hibernating during periods of food shortage in order to survive, but the evidence does not support this method. Since the hamster does not increase its body fat, even the inactivity during a hibernation period would still deplete too much energy, and the hamster would not survive. For this reason, Syrian hamsters are notoriously poor hibernators (Rowland, 1982). If hamsters cannot store body fat or hibernate, then perhaps the answer lies in external means of food storage, such as hoarding.

Hoarding does appear to be the method for which the Syrian hamster is best adapted. Evolution has designated this method of food storage to be useful for the hamster. Lea & Tarpy (1986) claim that the Syrian hamster is one of the best known, and possibly the most prolific, of hoarding animals. In many cases, organisms that engage in specific behaviors have physical adaptations to support the behavior.

Hamsters have an anatomical adaptation to hoarding in the form of large cheek pouches (Lea & Tarpy, 1986; Wong, R., 1984). These pouches expand and allow the animal to deposit food in them, necessitating fewer trips to the foraging site. The pouches extend around the side of the face down to the neck. Hamsters can carry up to half their body weight in their cheek pouches (Slaven, 2000). In addition to the physical cheek adaptation, hamsters also exhibit certain behavioral adaptations that complement hoarding behavior.

The living pattern of hamsters is a behavioral adaptation that is consistent with hoarding. Hamsters are solitary animals; they do not live and feed in groups. Andersson and Krebs (1978) found that hoarding is more widespread among species utilizing individual feeding areas because there is no competition for the food hoard and no other animals to rely on for food. Thus, when the hamster needs to hoard to survive, it is behaviorally equipped to do so. The determinants of hoarding, however, are not as obvious as the observable adaptations.

DiBattista and Bedard (1987) suggested various determinants for hoarding including exposure to cold temperatures, voluntary exercise, lactation, and insulin administration. Additional putative determinants include illumination and food deprivation, as suggested by both Charlton (1984) and Morgan (1947). The effects of food deprivation on hoarding behavior have been most widely studied and many researchers believe that food deprivation is the most important single factor in instigating hoarding behavior (Morgan, 1947; Wood & Bartness, 1996).

Recently, however, researchers have discovered that hamsters will hoard food even when they are satiated. Charlton (1984) made the observation that golden hamsters were able to acquire and perform a learned response (lever pressing) for food reinforcement without being food deprived. He also noted that these hamsters earned and pouched many more pellets than they ate; this suggests that nature determined the animals to hoard beyond physiological hunger. Thus, hunger is not the only determinant in food hoarding.

Morgan (1947) speculated that a different biological function that may induce hoarding in hamsters is stress. Stress can be defined as when environmental demands tax or exceed the adaptive capacity of an organism, resulting in biological changes that may place the organism at risk for disease (Cohen, Kessler, & Gordon, 1997). Note that all but one of the hoarding determinants listed above has to do with a lack of food energy available to the animal. A cold temperature means a scarcity of food; exercise, lactation, and insulin administration all have to do with eating and energy stores; food deprivation most definitely has to do with food consumption. It is possible, however, that these determinants are not important because they induce hunger, but because they increase the animals' stress response. If this were the case, then illumination would be the only determining factor that did not directly involve hunger, but did involve stress, and it would be important to look at the effects of illumination on hoarding.

To better understand the effects of illumination on hoarding, it is necessary to examine the possible reasons why illumination is stressful for the golden hamster. Researchers who have conducted studies involving illumination seem to agree that a light present in the foraging chamber is aversive to the hamster as evidenced by an increase in hoarding comparable to both a mild shock and food deprivation condition (Charlton, 1984; Bindra, 1948 as cited in Charlton, 1984). Not much detail is known regarding why this light is so unpleasant. The most likely explanation is that the presence of light makes the animal more visible to potential predators. Since hamsters are naturally nocturnal, feeding in a lighted area may increase the chance of predation.

Although little research on the effects of illumination exists, a few studies have suggested that illumination of the foraging area serves to increase hoarding behavior in the golden hamster (Charlton, 1984; Morgan, 1947). Charlton (1984) noted that illumination has effects similar to food deprivation or 0.1 mA of shock. The light creates a difference in security between the home cage and the foraging area because the animal is easily seen in the lighted foraging cage. The increase in stress response due to these factors, as seen in increased lever pressing during the session, appears to increase the amount of food hoarded by the hamsters (Charlton, 1984).

If further support were gathered to the effect that illumination of the foraging area is as powerful (or even more powerful) than the traditional food deprivation, this would be a very significant finding. It would offer another piece of the puzzle as to what determines hoarding behavior in hamsters. It would also provide additional options to researchers looking to reinforce their animals for studies. Hamsters are very difficult to food deprive because of their small size and failure to store body fat. Being able to use illumination instead of food deprivation would offer a safe alternative that would save time, money and animal lives.

The present study directly examined the effects of food deprivation and illumination on hoarding behavior, as well as the interaction between the two variables. Based on the previous findings, there were several expected outcomes. One hypothesis was that food deprivation should increase the amount of hoarding exhibited by the hamsters. A second hypothesis was that illumination should also increase hoarding behavior. It was uncertain, however, which of these factors would have a greater effect on hoarding or whether or not these variables would interact to affect the hoarding outcome.

Method

Subjects

The subjects were 12 male Syrian (Golden) Hamsters approximately 8 months of age, weighing from 101 g to 118 g. The animals were obtained from Harlan Sprague-Dawley and were housed individually in polycarbonate cages manufactured by Allentown Caging.

The animals were given free access to food (Harlan Teklad LM-485 Mouse/Rat sterilizable diet 7012) for 16 hours of the day (from 5 PM to 9 AM). Animals in the deprivation condition did not have access to the food from 9 AM until 5 PM, while the others did have free access until the start of the session at 4 PM. The animals were given the opportunity to hoard pellets from the Bio-Serv company, product # F05474-1. Each pellet measured one gram and contained 3.29 kcal. Water was made available, except for during the 30-minute session, through the stainless steel grated cage top.

Apparatus

The apparatus included a home cage, a connection tube, and an experimental cage. The home cage measured 26.7 cm in width, 48.3 cm in length, and 20.3 cm in height, which is the "standard shoebox" size for rats. These polycarbonate chambers from Allentown Caging had a floor area of 363.2 square cm. The animals were provided with 0.64 cm corncob bedding and PVC Sanitary "T" pipe, 5.1 cm in diameter. The connection tube was a standard piece of PVC piping. The tube was made out of PVC material plastic, was 5.1 cm long, and 5.1 cm in diameter. The foraging cage was a "shoebox" size mouse cage from Allentown Caging. The cage measured 19.1 cm by 29.2 cm and was 190.5 square cm. The 0.64 cm corncob bedding was also provided as well as a 5 X 6 matrix of food pellets along the bottom of the foraging chamber.

The humidity of the room in which the animals resided ranged from 30-70% and the temperature ranged from 65-70 degrees Fahrenheit. This is within the legal limits, requiring the temperature to remain between 64 and 78 degrees Fahrenheit at all times. The illumination cycle was also within the legal limits, with a 10:14 hour light/dark cycle, which is associated with particularly high levels of dark-phase hoarding (Jones & Pinel, 1990). Eight 32-watt bulbs provided illumination during the experiment. During the "light cycle," the room was brightened to an intensity of 325-400 lux. In the "dark" condition, the light intensity in the room was approximately 200 lux.

Procedure

Prior to the commencement of the study, a 10-day baseline period was conducted. The hamsters were weighed before and after the 30-minute sessions and all hamsters were tested under the same conditions (no cage illumination or food deprivation was employed). The food pellets were also counted before and after each session. It was noted whether food pellets missing from the matrix were consumed, hoarded in the home cage, pouched in the cheeks, or piled in another location within the foraging cage. (See attached appendix for detailed procedure outline).

The 12 subjects were split into 2 groups of 6 due to the limited number of experimental set-ups available. The 2 groups were run back-to-back, with a 10-day baseline preceding each group's experimental sessions. The 6 subjects in each group were randomly assigned to each of the four experimental conditions. The hamsters were rotated amongst the conditions such that each hamster participated in each condition only once. The conditions were defined as follows: Condition 1 involved testing the subjects with cage illumination and with food deprivation. Condition 2 involved testing the subjects with cage illumination and without food deprivation. Condition 3 involved testing the subjects without cage illumination, but with food deprivation. Condition 4 involved testing the subjects without cage illumination and without food deprivation. All subjects were housed in a room with a 10:14 hour light/dark cycle (with the light cycle beginning at 11 PM). This cycle offered the greatest opportunity for testing of the animals during the middle of their dark cycle (3 PM- 5PM). These subjects were tested during the middle of their light/dark cycle, as done in previous studies involving illumination (Charlton, 1984). Food was made available to "food deprived" hamsters up until

7 hours prior to the session. Previous studies have varied widely on the length of food deprivation, but in the experience of this lab, deprivation of more than 7 hours may lead to expiration of the animals.

All testing was done in the home cage, with the connecting tube opened to allow the hamster to freely move between the home cage and the foraging cage. Prior to each session, the hamsters were weighed and the food pellets were counted. The door blocking the connection tube, and thus the foraging cage, was opened to allow the hamsters access to the tube and foraging cage as well as the home cage. Each session was 30 minutes in length. At the end of the session any hamsters still in the foraging cage were removed by the experimenter and placed back in the home cage. At this time, the hamsters were weighed and the food pellets were counted once again. Hoarded food was removed from the home cage at the end of each session. Each hamster participated in each condition for 5 sessions each (for a total of 20 sessions per group of 6 hamsters).

Measures

There were 9 measures taken in this study. The first measure was called *Food Eaten* and was defined as the grams of food missing from the foraging cage, with the hamsters' cheeks remaining empty. The second measure was *Food Hoarded* and consisted of the grams of food moved from the foraging cage to the home cage. *Pellets Pouched* was the measure of the grams of food missing from the foraging cage when the hamsters' cheeks were full. *Total Pellets Moved* measured the grams of food piled or hoarded for each trial and *Avg Moved* refers to the average grams of food piled or hoarded across the five days of each condition. The measure *Total Food Handled* included all of the grams of food piled, hoarded, pouched, and eaten. The *# of Piles* was recorded for each hamster as well as the number of *Pellets per Pile*. The *# of Droppings* present in each foraging cage were also noted.

Results

Data from the 5 days of each condition were averaged for each subject for each of the response categories defined in the *Measures* section. These data were then combined into group averages, and are presented in Table 1. Note that some of the measurements in Table 1 are raw data averages, such as *Food Hoarded, Food Eaten, Pellets Pouched*, and *Number of Droppings*. The remaining measures are combined from two or more raw data measures; *Average Food Moved* is the sum of *Food Piled* and *Food Hoarded*; *Total Food Handled* is the sum of *Food Piled, Food Hoarded, Pellets Pouched*, and *Food Eaten.*

As seen in Table 1, the averages for *Food Hoarded* were very low. Only 2 of the 12 hamsters hoarded food consistently. Six of the hamsters hoarded sporadically. A two-factor within subjects Analysis of Variance (ANOVA) found no significant main effect of either illumination [F (1, 11])= 2.40; $p>0.05$] or deprivation [F (1, 11)= 1.64; $p>0.05$]. There was also no significant interaction [F (1, 11) = 2.54; $p>0.05$].

Although hamsters rarely hoarded, all hamsters moved the food from its original location (labeled *Average Food Moved* in Table 1), almost always placing it into piles in the foraging chamber. There was no significant main effect of illumination on food movement [F (1, 11) = 1.45; $p>0.05$]. There was, however, a main effect of deprivation, such that hamsters moved less food when food deprived than when not food deprived [F (1, 11) = 9.73; $p< 0.01$]. There was also no significant interaction [F (1, 11) = 1.01; $p>0.05$].

Table 1 also shows that there was less variation in the *Total Food Handled* measure. There was no significant main effect of either illumination [F (1, 11) = 2.58; $p>0.05$] or deprivation [F (1, 11) = 3.70; $p>0.05$]. There was also no significant interaction [F (1, 11) = 3.72; $p>0.05$].

Although there was not much variability in the amount of food handled by the hamsters, there were some differences with respect to how much food the hamsters consumed. There was no significant main effect of illumination on food consumption [F (1, 11) = 1.25; p>0.05]. There was, however, a main effect of deprivation, such that the hamsters ate more food when food deprived than when not food deprived [F (1, 11) = 24.93; p< 0.01]. There was also no significant interaction [F (1, 11) = 0.09; p>0.05].

In the *Pellets Pouched* measure, there was no significant main effect of either illumination [F (1, 11) = 1.41; p>0.05] or deprivation [F (1, 11) = 1.82; p>0.05]. There was also no significant interaction [F (1, 11) = 1.26; p>0.05].

In the *Number of Droppings* measure, there was a significant main effect of illumination, such that there were fewer droppings in the foraging cage in the presence of illumination [F (1, 11)= 14.16; p< 0.01]. There was no main effect of deprivation [F (1, 11) = 0.50; p>0.05] and there was no significant interaction [F (1, 11) = 0.07; p>0.05].

In summary, there was a main effect of illumination for the number of droppings found in the foraging chamber; there were main effects of deprivation for both food moved and food eaten. There were no significant interactions between any of the measures.

Discussion

The present study examined the effects of illumination and food deprivation on hoarding behavior in the golden hamster. Food was rarely moved from the foraging cage to the home cage, and no significant differences in this "true" hoarding were found across conditions. The amount of food moved from its original location decreased significantly as a function of food deprivation, but not as a function of illumination. In addition, the number of droppings found in the foraging cage decreased as a function of illumination. The present results do not confirm predictions, nor do they replicate previous studies. Based on previous research, an increase in food hoarding would have been expected in both the illumination and deprivation conditions; the number of droppings would also have been expected to be greater in these two conditions.

The results suggest that food deprivation did affect the amount of food movement, regardless of the presence of illumination. However, the direction of the effect was opposite to what previous literature might suggest (Charlton, 1984; Morgan, 1947). That is, the presence of food deprivation was shown to decrease the amount of food moved during the sessions, relative to the absence of food deprivation. There was also a slight but significant increase in food consumption during the food deprivation sessions, making it clear that the procedure was successful in inducing a deprivation state. Although this finding was logical, some of the results were not as clear-cut.

The present data also failed to show an effect of illumination on the amount of food movement or food consumption. Illumination did have an effect on the number of droppings found in the foraging cage. This "Number of Droppings" measure was designed to test for stress levels. The number of droppings in the foraging cage decreased as a function of illumination, which is contrary to what previous literature would suggest (Hashiguchi et al, 1997). This is a perplexing finding. The hamsters in the present study were apparently less stressed when illumination was present than when it was absent.

Another possibility is that the droppings category was a poor measure of stress. Because the home cage was only cleaned out once a week, it was difficult to count all of the droppings in the home cage as well as the foraging cage. It is possible that the hamsters went back to the home cage in order to defecate if they were indeed stressed by the deprivation and/or the illumination conditions. This is a definite limitation of this study. More research would need to be done to definitively determine what this finding means.

The present study did not find an interaction between illumination and deprivation for any behavioral measure. The effects of illumination on hoarding did not vary depending on the level of deprivation; likewise, the effects of deprivation did not depend on the level of illumination. The potential interaction effects were a unique feature of this study, and therefore cannot support or contradict previous research findings. However, there may be reasons why the individual manipulations failed to replicate prior results.

The present experiment may have failed to replicate previous results with regards to deprivation for several reasons. Other literature on hoarding behavior in hamsters used deprivation periods ranging from 12 hours (Jones & Pinel, 1990) to 72 hours (Rowland, 1982). Perhaps the low levels of deprivation used in the present study served only to increase hunger in the animal, but was not effective in producing significant food movement. As stated earlier, however, it was the opinion of this lab that a longer deprivation period may have endangered the health of the hamsters.

It does make logical sense, however, that the hamsters might spend less time hoarding and more time eating when they are mildly food deprived. In this situation, the animals are hungry so they take advantage of the available food to satisfy that immediate need. Perhaps it is because of the low level of food deprivation used here that the hamster did not feel the urge to hoard the food for later consumption. Another possibility is that the hamsters somehow sensed the season and chose not to hoard for that reason. Since data was collected in the spring, this would not be the time of year that these animals would usually hoard. Instead this would be the time for free feeding or eating off the hoard that had been stored for the winter months. It is the case, however, that this study did not find effects of "true" hoarding, which may have impacted the animals' decision to eat.

Of particular interest is the failure to find "true" hoarding as defined previously. The behavior category "food movement" is used instead of "hoarding" because the majority of hamsters did not engage in "true" hoarding; thus, the hamsters were not moving food from the foraging chamber to the home cage, but instead moving it from its original location within the foraging chamber. It is important to examine why this may be the case.

One possible explanation for the lack of "true" hoarding is that, as previously mentioned, the deprivation period was not sufficient to produce the urge to hoard. If stress plays a role in hoarding behavior, as suggested in previous literature (Charlton, 1984), then perhaps a 7 hour deprivation period does not produce a high enough level of stress in the animal. Future studies need to consider an increased deprivation period under careful supervision to find support for this claim.

A second explanation for the lack of hoarding may be that the foraging chamber was more attractive to the hamsters than their home cage. This follows from the work of Charlton (1984) who suggests that aversive qualities of one environment lead the animal to hoard food in a more pleasant environment. Although the home cage had the odor of the hamster occupant, the foraging chamber was darker (an appealing quality to nocturnal hamsters) and it was cleaner (the foraging chamber was cleaned daily and the home cage was cleaned weekly). In addition, the foraging cage was also smaller and more conducive to resting/ hiding because it was opaque, rather than clear like the home cage. Future research may consider placing a type of darkened, enclosed area in the hamster's home cage which the animal could then bring hoarded food back to. The animal may find this type of area to be less stressful, due to the decrease in light, if stress is what is acting here. In addition to these lighting concerns, there may also be other explanations for the non-significant illumination findings.

There are two other possible explanations for the lack of a significant illumination effect on food movement. First, the light may not have been intense enough to induce stress in the animals. Intensifying the light source may be a consideration for future studies. Second, light from the "illumination" side of the testing room may have flooded into the "dark" side of the room, causing less of a difference between these two conditions. This situation could be alleviated by either housing "illumination" and "dark" subjects in separate rooms or having a barrier on the dark side to block out any incoming light. Based on these possible limitations, it is clear that further research needs to be conducted on this topic.

Another limitation of this study involves the lack of a "natural" environment provided in this lab setting. In nature, hamsters are able to burrow into the dark underground to store their food; providing the dark enclosure in the home cage may help to simulate this effect. However, it is not plausible to offer a natural type of burrowing environment in a laboratory setting. Another natural occurrence involves light cycle patterns that alert the animal to particular seasons. In this study, the hamsters were inadvertently alerted to the winter light cycle because of the 10:14 hour light/dark cycle set in the lab. This may have been an additional factor that hindered the hoarding behavior of the hamsters since summer would be the time that hamsters would hoard (to prepare for the winter months ahead). Based on these various limitations, further research needs to be done to determine the true determinants of hoarding.

Future research on hoarding behavior in hamsters needs to identify whether hunger itself is a determinant of hoarding, or whether hunger leads to an increased stress level. More specific and conclusive measures such as cortisol blood levels could be used to measure the animals' stress level. Access to measures such as this would be immensely helpful in determining the true stress level of the hamsters. By simply measuring the cortisol levels in the blood during a food deprivation period, the researcher would be able to tell whether or not the animals' stress levels had increased. This would help to answer why food deprivation had the effect of decreased food movement in this study. It still remains to be determined whether a decrease in food movement is actually present in the presence of food deprivation or whether this only occurs at low levels of deprivation, as seen in this study.

Other potential stressor variables in addition to illumination such as shock, social reorganization, etc. need to be examined further to determine their effects on hoarding behavior. Similar to the suggestion with food deprivation, blood cortisol levels would also be useful here. It would be interesting to see if, under the right conditions, deprivation, illumination, and shock could all induce equal amounts of stress, and thus hoarding in the hamsters. In addition, interactions could be studied at that point, with stress levels from each separate manipulation being equal.

In conclusion, the present study found some significant effects, but provides more questions than answers. The results obtained from the present study were not conclusive in identifying the hoarding behavior of golden hamsters under the conditions of food deprivation and illumination. This is particularly true because all of the significant findings in this study were contrary to the previous research. It is not clear why the present study did not replicate earlier work, though several reasons have been suggested. Future research will need to clarify the contradiction between the present findings and previous studies. Additional research should also examine other dimensions of hoarding behavior.

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Appendix

Experimental Procedure for 30-minute Hoarding Sessions

1. Light is turned on "illumination" side (left side)
2. Hamster is removed from home cage
3. Hamster is weighed and returned to home cage
4. Cage lid is replaced with empty lid
5. Cap is removed from tube and time starts
6. Weight is recorded
7. Steps 1-5 are repeated for each hamster (3 minutes b/w each hamster)
8. Hamster is removed from foraging chamber and cap is replaced after 30 minutes
9. Hamster is weighed
10. Weight is recorded
11. Food is removed from home cage
12. Steps 9-10 are repeated for each hamster (at 3 minute intervals)
13. Food in foraging chamber is counted, total and per pile
14. Food weight is recorded for food consumed, pouched, piled in foraging chamber, and hoarded in the home cage
15. Hamster droppings from foraging chamber are counted
16. Number of droppings is recorded
17. Food is returned to 6 x 5 matrix with volume restored to 30 pellets

Table 1

Means (Standard Deviations) for Various Measurements Across the Four Conditions

		Condition		
Measurement	I & D	I	D	Control
Food Hoarded	3.68 (7.88)	8.10 (10.78)	3.23 (6.82)	2.55 (8.55)
Average Food Moved*	24.85 (3.08)	25.57 (4.06)	22.88 (4.63)	25.78 (1.86)
Total Food Handled	26.61 (3.05)	26.17 (4.09)	23.75 (4.62)	26.65 (2.07)
Food Eaten*	0.68 (0.21)	0.45 (0.18)	0.63 (0.21)	0.32 (0.19)
Pellets Pouched	0.76 (2.43)	1.03 (0.28)	0.27 (0.56)	0.17 (0.31)
Number of Droppings**	0.40 (0.40)	0.62 (1.09)	1.20 (1.44)	1.53 (1.34)

* Significant main effect of deprivation, $p < 0.01$

** Significant main effect of illumination, $p < 0.01$