Differences in hoarding behavior between captive and wild sympatric rodent species

Hongmao ZHANG1,2*, Yu WANG2

1 Laboratory of Ecology and Evolutionary Biology, College of Life Science, Central China Normal University, Wuhan 430079, China
2 Institute of Zoology, the Chinese Academy of Sciences, Beijing 100101, China

Abstract  In hand reared birds and mammals, it is generally considered that the development of hoarding behavior is the result of an interaction between the development and maturation of the nervous system and learning from individual experience. However, few studies have been done on wild animals. We tested differences in hoarding behavior between captive reared and wild individuals of two sympatric small rodents, Korean field mice *Apodemus peninsulae* and Chinese white-bellied rats *Niviventer confucianus*. Our aim was to identify if lack of experience from the wild would result in poorly developed hoarding behavior. The Korean field mice perform scatter- and larder-hoarding behaviors whereas Chinese white-bellied rats hoard food in larders only. Within outdoor enclosures we compared seed-hoarding behavior in reared juveniles (RJ, 40-50 d old, pregnant mothers were captured in the wild), wild juveniles (WJ, as young as the RJ) and wild adults (WA, over-winter animals). We found that a lack of experience from the wild had significant effects on seed-hoarding behavior for both species. The RJ-group removed and hoarded fewer seeds than the WJ- and WA-groups. The two latter groups hoarded seeds in a similar way. In the Korean field mouse the RJ-group placed more seeds on the ground surface than other groups. These findings suggest that wild experience is important for the acquisition of an appropriate food-hoarding behavior (especially for scatter-hoarding) in these species [Current Zoology 57 (6): 725–730, 2011].

Keywords  Behavioral ontogeny, Food-hoarding behavior, Instinct, Learning, Practice, Social experience

Food-hoarding involves the performance of complex behaviors and stereotyped sequence of acts that seems to have its ontogenetic processes in food-handling behavior (Vander Wall, 1990). The ontogeny of hoarding behavior has been investigated in several birds and rodents such as loggerhead shrikes *Lanius ludovicianus* (Smith, 1972), crested tits *Parus cristatus* and willow tits *Parus montanus* (Hafforn, 1992), marsh tits *Poecile palustris* (Clayton, 1996), golden hamsters *Mesocricetus auratus* (Etienne et al., 1982, 1983) and European ground squirrels *Spermophilus citellus* (Heschl, 1993). However, this question has been largely ignored in recent years (but see Pollok et al., 2000; Bugnyar et al., 2007). As a result detailed examples that illuminate the process of the behavioral ontogeny of hoarding remain scant.

When it comes to how hoarding behavior is acquired, some researchers have emphasized the significance of instinctive capacities (reviewed by Vander Wall, 1990; Steele et al., 2006). Some species of rats show species-typical forms of hoarding behavior elicited in food deprivation conditions, not through training (Vander Wall, 1990), and some squirrels (e.g. grey squirrels *Sciurus carolinensis*) express a strong innate basis for some hoarding decisions (e.g. embryo excision) (Steele et al., 2006). Other studies maintained the significance of learning experiences (e.g. Bevan and Grodsky, 1958). Particularly, early experiences (during the 2nd to 6th months of life in some species of bird and mammal) contribute significantly to performances of hoarding behavior in adults (Bevan and Grodsky, 1958; but see Heschl, 1993). For example, juvenile golden hamsters and laboratory reared rats with experiences of handling food pellets perform as well as adults and hoard significantly more than inexperienced individuals (Holland, 1954; Bevan and Grodsky, 1958). These two views may be reconciled by considering that the coordination of hoarding behavior is the result of interactions between developmental processes corresponding to maturation of the nervous system and learning from individual experience (Vander Wall, 1990). Variability in hoarding performance is partially influenced by environmental conditions (e.g. territory quality and social interactions), but to what extent is determined by genetic factors.
(Vander wall, 1990; Haftorn, 1992). Under natural conditions, juveniles, especially for social group-living species, can learn food-hoarding tactics from their parents or other experienced individuals (e.g. Norway rats *Rattus norvegicus*, Galef et al., 1983; crested tits and willow tits, Haftorn, 1992). The process of learning is very important for hoarders to develop food-hoarding behavior (Vander Wall, 1990). Much of what we know about innate versus learning in hoarding behavior acquisition has been conducted on birds and some captive rodents, (reviewed in Vander Wall, 1990; Haftorn, 1992; Bugnyar et al., 2007). Very few studies have been conducted on mammals under natural conditions or in outside arenas.

We tested seed-hoarding behaviors in two sympatric rodent species, Korean field mice *Apodemus peninsulae* and Chinese white-bellied rats *Niviventer confucianus*, from different cohorts, with different wild experience (reared juveniles, wild juveniles and wild adults) under semi-natural enclosure conditions. We asked whether the lack of wild experience might result in poorly developed seed-hoarding behavior. Due to the experience-reliable mechanism of hoarding behavior development, we hypothesized that wild inexperienced animals (reared juveniles) would perform seed-hoarding poorly compared to wild animals.

### 1 Materials and Methods

#### 1.1 Experimental animals

Korean field mice and Chinese white-bellied rats are common rodent species at the Liyuanling field station (40°00′N, 115°30′E, ca. 1,100 m a.s.l.; ca. 120 km northwest of Beijing city) in the Donglingshan Mountains where we carried out this study (also see Li and Zhang, 2003, 2007; Zhang et al., 2008; Huang et al., 2011). They vary in body size (Korean field mice: 80–135 mm body length, 20–35g body weight; Chinese white-bellied rats: 125–195mm body length, 45–150g body weight; adults; also see table 1) but share similar daily active rhythm, diets and habitats in the study area (Li et al., 2004). Pups (4–6 per litter) of the two species are weaned within 30 days and mature within 60 days (Zhang H unpublished data). Korean field mice perform both scatter- and larder-hoarding behaviors, whereas Chinese white-bellied rats only larder hoard food items (Lu and Zhang, 2008; also see table 1). These species are ideal for examination as they are common, easily maintained in the laboratory and the subjects of previous studies (e.g. Lu and Zhang, 2008; Zhang and Wang, 2009; Huang et al., 2011).

Animals from each species were assigned to one of three groups (Table 1): (1) reared juveniles (RJ): animals were born in laboratory and reared in captive conditions, their pregnant mothers were captured in wild; (2) wild juveniles (WJ); and (3) wild adults (WA): over-winter animals. We identified the ages of subjects by fur color and body weight (Wilson and Reeder, 2005). Wild trapped animals with light grey fur and small bodies (<20 g in Korean field mice and ≤55 g in Chinese white-bellied rats) were classified as WJ (as young as RJ), while those with light yellowish-brown fur and a large body (>20 g in Korean field mice and >60 g in Chinese white-bellied rats) were placed in the WA group. The WA provides a control for the effects associated with wild experience, while the WJ provides a control for effects related to age. If the RJ performs more poorly in hoarding than WJ and WA, a lack of wild experience would perform negative effects on acquisition of hoarding behavior of the subjects.

Animal trapping was conducted using steel-wire live traps (12 × 12 × 25 cm³) (described by Xiao et al., 2008; Zhang et al., 2008; Lu and Zhang, 2008; Huang et al., 2011). Captured animals, except for lactating animals released immediately on site, were transferred to the laboratory using live traps. Korean field mice and Chinese white-bellied rats were raised separately in different rooms using individual plastic boxes (37 × 26 × 17 cm³) at ambient temperature (18–25°C) and photoperiod (ca. 12:12 h light: dark cycle). Commercial mouse chow (Keao Feed Ltd., Beijing, China), water and nest substrates were available ad libitum. Peanuts (10–15 g per animal per day) and cotton were provided as extra nutrition supplements and warm materials to pregnant females during the period of pregnancy and lactation. Sex, body weight, breeding-status (pregnancy) and age of captured animals were recorded. Only non-breeding individuals were used in enclosure tests. All experimental individuals were maintained in the laboratory under similar conditions for at least one week and food deprived for 12 h (to ensure that all subjects were highly motivated to store) prior to hoarding trials. After this study, animals were retained for other studies. Animal trapping and use complied with the guidelines for animal use and care as stipulated by the Institute of Zoology, Chinese Academy of Sciences (also see Zhang and Wang, 2009; Huang et al., 2011).

#### 1.2 Seed marking

Wild apricot shrubs are widely distributed throughout the study area. Their seeds (1.2±0.2 g weight, 22.1±1.6 mm long, 9.8±0.8 mm wide, mean±SD, n = 50, includ-
ing endocarps) are favored food items for the focal animals because of their high nutritional content (53.1% crude fat, 25.5 J/g caloric value for kernels), and are ideal food for testing hoarding behavior (Zhang and Zhang, 2008; Lu and Zhang, 2008; Huang et al., 2011). Experimental seeds were collected in a secondary forest and marked following the tin-tag method: a unique coded tin-tag (3.0 × 1.0 cm², ca. 0.1g) is tied to each seed using a piece of fine steel wire (ca. 3 cm long) (Zhang and Wang, 2001). This method is widely used in tracking rodent-dispersed seeds both in the wild and enclosures (e.g. Xiao et al., 2006; Gómez et al., 2008; Yi et al., 2008, Huang et al., 2011).

1.3 Enclosure design

Four outdoor enclosures (9 × 9 × 1 m³) were constructed using bricks in open places and covered with wire mesh (1 × 1 cm² grid) to prevent animals from entering or escaping. Some grass (e.g. Artemisia Linn Spp., Poa spp., ca. 30 % for plant coverage) was grown inside enclosures to simulate the surrounding environment. Soil inside enclosures was raked prior to each trial to aid hoarding. A wooden nest box (18 × 40 × 18 cm³) and a water plate (10 cm in diameter) were placed in one corner. Experimental seeds were placed in the centre (seed station, ca. 0.5 m² wide) of enclosures (Zhang and Zhang, 2006, 2007; Lu and Zhang, 2008).

1.4 Experimental protocol

Experiments were conducted during the peak time (September to October) of seed-hoarding (2006 for Korean field mice and 2008 for Chinese white-bellied rats) (Zhang H, personal observation).

Thirty seeds per night were offered to each animal for eating and hoarding (each subject consumed approximately ten seeds per night in captivity). Each trial lasted one night (ca. 24 h) following the protocol: after seed placement, one subject was introduced into the enclosure (14: 00–15: 00 hours) and removed the next morning (11: 00–12: 00 hours). All seeds and their fragments were removed from enclosures after allocation to one of four categories: (1) eaten (kernels are consumed with tag or seed fragments are left on ground surface or in nest); (2) scatter-hoarded (intact seeds are buried in soil); (3) larder-hoarded (intact seeds are in nest); and (4) intact after removal (intact seeds are laid on ground surface after removal). The sum of the above four categories of seed were defined as ‘the total number of removed seeds’ (Huang et al., 2011). Substrate soil was raked and new nest box and water plate were provided. Tests were conducted 24 h apart to weaken the olfactory cues left behind by animals.

1.5 Statistical analysis

The number of seeds (per animal per night) attributable to each seed fate was used as a measure of hoarding intensity (Huang et al., 2011; Cheng and Zhang, 2011). SPSS for Windows (SPSS Inc., Chicago, USA) was used for conducting data analyses. Indexes of Skewness and Kurtosis were used to explore the normal distribution of all data. A Kruskal-Wallis Test was used to compare differences of each seed fate among three groups (RJ vs WJ vs WA). A Mann-Whitney Test was used to determine differences for each seed fate between groups (RJ vs WJ, RJ vs WA and WJ vs WA).

2 Results

2.1 Korean field mice

There was an effect of a lack of wild experience on seed-hoarding behavior in Korean field mice. The total number of removed seeds (χ² = 7.787, df= 2, P = 0.020) and scatter-hoarded seeds (χ² = 24.526, df = 2, P < 0.001) were significantly different among the three categories of animals. The RJ removed fewer seeds from seed stations (RJ vs WJ: Z = -2.056, P = 0.041; RJ vs WA: Z = -3.079, P = 0.001), did not scatter hoard (RJ vs WJ: Z = -4.163, P < 0.001; RJ vs WA: Z = -4.911, P < 0.001) but placed more seeds on the ground surface (RJ vs WJ: Z = -2.119, P = 0.034; RJ vs WA: Z = -2.106, P = 0.045) than WJ and WA. Hoarding behaviors were similar for WJ and WA (all P > 0.05) (Table 1).

2.2 Chinese white-bellied rats

There was an effect of a lack of wild experience on seed-hoarding behavior in Chinese white-bellied rats. The total number of removed seeds (χ² = 15.268, df= 2, P = 0.001) and larder-hoarded seeds (χ² = 20.925, df= 2, P < 0.001) were significantly different among the three categories of rats. The RJ group removed fewer seeds from seed stations (RJ vs WJ: Z = -3.379, P = 0.001; RJ vs WA: Z = -3.352, P = 0.001) and hoarded fewer seeds in larders (RJ vs WJ: Z = -4.117, P < 0.001; RJ vs WA: Z = -3.457, P = 0.001) than the WJ and WA. In addition, the RJ group placed more seeds on the ground surface than WA (Z = -2.217, P = 0.027). Hoarding behaviors were similar for WJ and WA (all P > 0.05) (Table 1).

3 Discussion

As predicted, a significant effect of a lack of wild experience was found on seed-hoarding behavior in Korean field mice and Chinese white-bellied rats. This experience-gained strategy in food-hoarding has been reported by earlier studies (e.g. Holland, 1954; Bevan
were kept in individual after weaning (20 – 25 days old) and were used in tests when they are 40-50 days old.

Each column, different superscripts indicate significant difference (P < 0.05).

Observations in adult birds, juvenile pinyon jays (Stotz, 1991). Food-hoarding involves a complex of behaviors that are strongly influenced by social experience (Bugnyar et al., 2007). Before expressing skilled hoarding behavior in adult birds, juvenile pinyon jays Gymnorrhinus cyanoccephalus require exposure to a large group of jays hoarding seeds (Stotz, 1991). In our study, reared juveniles were isolated and maintained under laboratory conditions after weaning. This social isolation prevented subjects from learning each other; they were especially deprived of the chance to learn from their experienced parents. Animals raised without parents may show a variety of severe deficits in social interactions (Bertin and Richard-Yris, 2005) and a reduced ability for social learning (Lévy et al., 2003). Therefore, the lack of social experience in hand reared juveniles might result in poor hoarding behavior, although we did not test this directly. However, the effect of social experience on some species’ hoarding behavior is not as significant as we expect. For instance, learning through imitation or even through instruction by the mother turns out to be not an important factor for ontogeny of seed harvesting techniques in developing European ground squirrels (Heschl, 1993). The early social environment influences the development of stereotypic behavior in adulthood (Jones et al., 2010). There is often a ‘critical period’ (between the 2nd and 6th month of life in many birds and mammals) for hoarding behavior development in many species (Vander Wall, 1990). If our focal animals are involved in these cases, the isolated feeding after weaning in 30 day old animals may cut off social learning during the ‘critical period’ of hoarding behavior development, and result in poor hoarding behavior in captive reared individuals. Another reason for poor hoarding behavior in reared juveniles may be the lack of practice with hoarding. Vander Wall (1990) shows that food hoarding behavior can be improved by practice in some birds and rodents. If animals (such as the reared juveniles in this study) are maintained with ad libitum food, under controlled temperature and other climate conditions, the natural motivational system to hoard will never arise, as happens in the wild. This in turn would lead to a lack of practice, and therefore a lack of this behavior. This prediction requires further observation because it is unclear whether the hand reared juveniles can hoard as well as wild individuals after practicing with hoarding under laboratory conditions. Hoarding behaviors in some species of rats are not elicited through training (reviewed by Vander Wall, 1990).

Our results may suggest that wild experience is a requirement for acquisition of food-hoarding behavior in some rodents. A similar result was observed in pinyon jays (Stotz, 1991). Food-hoarding involves a compli-

| Species                  | Groups | Samples | Body weight (g, mean±SD) | Captured time | Seed-hoarding (No. mean±SD) |
|--------------------------|--------|---------|--------------------------|---------------|-----------------------------|
|                          |        |         |                          |               | R | E | SH | LH | IR |
| Apodemus peninsulae       | RJ♀️    | 16 (♀️ 8♂️) | 19.2±2.5                 | Apr. to May, 2006♀️ | 10.7±5.9♀️ | 4.4±3.2♀️ | 0♀️ | 2.8±4.4♂️ | 3.2±2.8♂️ |
|                          | WJ♀️    | 16 (♀️ 4♂️) | 16.2±1.3                 | Sep. to Oct., 2006 | 15.9±8.7♂️ | 3.4±1.8♂️ | 6.6±6.1♀️ | 5.2±5.0♀️ | 0.8±0.9♀️ |
|                          | WA♀️    | 16 (♀️ 8♂️) | 24.1±3.7                 | Sep. to Oct., 2006 | 16.5±4.9♀️ | 4.3±2.9♀️ | 6.3±4.4♀️ | 5.0±3.6♀️ | 0.9±1.0♀️ |
| Niviventer confucianus    | RJ♂️    | 12 (♂️ 5♀️) | 49.4±3.8                 | Jul., 2008♂️ | 5.4±2.5♂️ | 2.9±1.5♂️ | - | 3.1±1.5♀️ | 1.4±1.4♀️ |
|                          | WJ♂️    | 12 (♂️ 7♀️) | 53.2±4.5                 | Sep. to Oct., 2008 | 14.2±7.3♀️ | 2.5±2.4♀️ | - | 10.5±5.7♀️ | 1.1±1.2♀️ |
|                          | WA♀️    | 12(♀️ 7♂️) | 73.1±1.8                 | Sep. to Oct., 2008 | 12.8±6.6♀️ | 5.2±4.5♀️ | - | 7.3±5.0♂️ | 0.3±0.7♀️ |

R: reared juveniles. WJ: wild juveniles. WA: wild adults. ♂️ Pregnant mothers were captured in wild and delivered in 1-2 weeks in laboratory. Pups were kept in individual after weaning (20 – 25 days old) and were used in tests when they are 40-50 days old. From six mothers. From five mothers. Times when the pregnant mothers were captured. R, total removed; E, eaten; SH, scatter-hoarded; LH, larder-hoarded; IR, intact after removal. For each column, different superscripts indicate significant difference (P < 0.05).
icated process that requires hoarders to take many factors into account and master multiple skills (Vander Wall, 1990; Preston and Jacobs, 2005; Hopewell et al., 2008). Hoarding skills would be polished during learning-practice interaction in the wild (Haftorn, 1992). Stafford et al. (2006) found that eight month old pinyon jays with two months or five months experience in their natural habitat showed equal hoarding ability as adult birds. The fact that reared juveniles performed poorly compared to wild juveniles and adults in seed-hoarding in this study may be because of the lack of wild practice with hoarding. However, we do not know if the reared animals can hoard as well as wild individuals after a period of training with hoarding under captive conditions. If so, experience, instead of wild experience, is a requirement for the acquisition of food-hoarding behavior in our focal species. Our interpretations need further investigation.

The reared Korean field mice juveniles, unlike wild juveniles and adults, did not hoard seeds in scatter, but placed more seeds on the ground surface. Caching of seeds on the soil surface is a type of scatter-hoarding (e.g. deer mice Peromyscus maniculatus, Vander Wall et al., 2001). Reared Korean field mice juveniles placed many seeds on the soil surface and suggests they appear to scatter hoard seeds, but perform poorly because of a lack of experience. Scatter hoarders often need a larger area and sufficient suitable sites for hoarding. Under isolated captive conditions, animals have no place to practice scatter-hoarding skills. However, we did not test this predication directly or find any reference to this idea in the literature. It is interesting that inexperienced mice placed seeds on the ground surface while experienced animals buried caches in soil. Burying food in the soil is a common strategy in pilferage avoidance (Dally et al., 2006), and food loss would stimulate scatter-hoarding intensity in Korean field mice (Huang et al., 2011). Scarcity of pilferage pressure may be one of the reasons for poor scatter-hoarding (seeds on the soil surface) in captive mice.

Overall, our results suggest that a lack of wild experience negatively influences the acquisition of food-hoarding behaviors in Korean field mice and Chinese white bellied rats. Under natural conditions many factors such as social context, learning, food availability and pilferage may affect the acquisition of hoarding behavior in rodents. Our results do not reveal which factor is mainly responsible for a poor hoarding performance in reared juveniles, and further experiments are required.

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