



Scatter hoarding and cache pilferage by superior competitors: an experiment with wild boar, *Sus scrofa*



Lennart Suselbeek^{a,*}, Vena M. A. P. Adamczyk^a, Frans Bongers^a, Bart A. Nolet^b, Herbert H. T. Prins^a, Sipke E. van Wieren^a, Patrick A. Jansen^{a,c}

^a Department of Environmental Sciences, Wageningen University, Wageningen, The Netherlands

^b Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

^c Smithsonian Tropical Research Institute (STRI), Balboa, Ancón, Panama

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Food-hoarding patterns range between larder hoarding (a few large caches) and scatter hoarding (many small caches), and are, in essence, the outcome of a hoard size–number trade-off in pilferage risk. Animals that scatter hoard are believed to do so, despite higher costs, to reduce loss of cached food to competitors against which they cannot defend their food reserves (henceforth: superior competitors). We tested the underlying assumption that the cost of having more caches under scatter hoarding, thus increasing the likelihood of cache encounter by superior competitors, is outweighed by the benefit of having small caches that are less likely to be detected upon encounter by superior competitors. We carried out a controlled experiment in which we distributed a fixed number of acorns over a fixed number of patches within a fixed area, varying cache size and cache depth, thus mimicking alternative hoarding patterns. We then recorded cache pilferage by a fixed number of wild boar, a well-known pilferer of acorn caches. The time wild boar needed to pilfer the first cache was shortest for scatter hoarding, but the time needed to pilfer all caches was slightly longer for scatter hoarding than for larder hoarding. Overall, however, the rate of pilferage did not differ between scatter hoarding and larder hoarding, and was not affected by cache depth. We conclude that the effects of alternative hoarding patterns on reducing cache pilferage by wild boar were smaller than expected, and that superior competitors may thus not be important drivers of scatter hoarding. Instead, other factors, such as conspecific pilferage or the risk of cross-contamination of food items in large caches, which can also cause catastrophic loss of food reserves, may be more important drivers of scatter hoarding.

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Many seed-eating animals cache seeds at times of high food availability and rely on these reserves during periods of food scarcity (Vander Wall, 1990). The spatial pattern at which seeds are cached ranges between larder hoarding and scatter hoarding (Vander Wall, 1990). Larder hoarding involves the placement of food items in one or a few caches ('larders'), usually located in or near the nest, in burrows or in tree cavities, that are often actively defended. Scatter hoarding, in contrast, involves spreading food over many widely spaced caches with one or a few items each ('scatters'), scattered throughout the hoarder's territory, usually created and accessed from the soil surface (Clarkson, Eden,

Sutherland, & Houston, 1986; Morris, 1962; Vander Wall, 1990, 2001).

Both hoarding strategies have their own set of advantages and disadvantages. Larders are relatively easy to create and recover, yet usually require active defence against other animals, which costs time and energy, involves risk of injury and is successful only if the hoarder is superior to its competitors (Clarkson et al., 1986; Dally, Clayton, & Emery, 2006; Daly, Jacobs, Wilson, & Behrends, 1992; Vander Wall, 1990). Moreover, larders emit stronger odours; hence, for competitors, larders may be easier to detect by olfaction than small caches. Scatter hoarding, by contrast, involves higher energetic costs in terms of travel (food is spaced out more widely) and memory (more locations have to be remembered), as well as increased mortality risk (longer exposure to predators and adverse environmental conditions) (Dally et al., 2006; Stapanian & Smith, 1978, 1984). Scatter hoards, however, are not usually defended individually (Jenkins, Rothstein, & Green, 1995; Smith & Reichman, 1984).

* Correspondence: L. Suselbeek, Department of Environmental Sciences, Wageningen University and Research Centre, PO Box 47, 6700 AA Wageningen, The Netherlands.

E-mail address: lennart.suselbeek@wur.nl (L. Suselbeek).

Given a certain number of food items to be hoarded, and a limited number of patches suitable for hoarding within a limited area (i.e. the home range), the hoarder's options are constrained, because reducing the number of food items per cache can only be done by increasing the number of caches and vice versa (Dally et al., 2006; Vander Wall & Jenkins, 2003). Thus, in essence, the decision about how to hoard a given number of food items is the outcome of a hoard size–number trade-off, in which hoarders optimally balance the risks associated with having a few large caches (i.e. larder hoarding) against the risks associated with having many small caches (i.e. scatter hoarding) (Alpern, Fokkink, Lidbetter, & Clayton, 2012; Hirsch, Kays, & Jansen, 2013). For many rodent and bird species, this balance is shifted towards scatter hoarding, presumably because they have competitors against which they cannot defend larders (henceforth: superior competitors; e.g. Brodin, Lundborg, & Clark, 2001; Dally et al., 2006; Daly et al., 1992; Hurly & Robertson, 1987; Stapanian & Smith, 1978; Vander Wall & Jenkins, 2003). Although for some species this may be a flexible context-dependent decision made on an individual level, for others changes in hoarding patterns may have evolved over time. That is, a population of hoarders that has been exposed to superior competitors for a long period of time may have evolved different hoarding patterns from hoarders of the same species that have not been exposed to superior competitors (e.g. Andersson & Krebs, 1978; Brodin, 2010; Dally et al., 2006; Levey, Silva, & Galetti, 2002; Siepielski & Benkman, 2008; Smith & Reichman, 1984; Stapanian & Smith, 1978; Vander Wall, 2001; Vander Wall & Jenkins, 2003).

There are two hypotheses regarding the mechanisms by which scatter hoarding could reduce the risk of cache pilferage (Dally et al., 2006). The assumptions underlying the first hypothesis (here termed the 'risk spreading' hypothesis) are that potential pilferers use random search or explorative search to find hidden food items and that larder hoarding involves the catastrophic risk of instantaneously losing the entire food supply (i.e. complete pilferage), imperilling the animal's survival (Wauters, Suhonen, & Dhondt, 1995). Scattering food items over many small caches spreads the risk of pilferage and thus makes complete pilferage less likely (e.g. Dally et al., 2006; Devenport, Luna, & Devenport, 2000; Jacobs, 1992; Kraus, 1983; Macdonald, 1997). For instance, consider 100 repeated trials of a pilferer randomly visiting a fixed number of 50 patches (and potentially revisiting some) out of a total of 100 patches. The probability of this pilferer encountering all caches is approximately 80% if the total number of caches is 2, whereas it is only 7% if the total number of caches is 32. Thus, simply increasing the number of caches should reduce the risk of complete pilferage if the pilferer operates by means of random search or explorative digging (Dally et al., 2006; Gálvez, Kranstauber, Kays, & Jansen, 2009; Vander Wall, 1990). The assumption underlying the second hypothesis (here termed the 'cue reduction' hypothesis) is that potential pilferers use special cues to locate hidden food items. It posits that scattered food is more difficult to detect and pilfer, for example because smaller caches are less easily detected by olfactory cues (e.g. Geluso, 2005; Reichman & Oberstein, 1977; Vander Wall, 1993b, 1998, 2000, 2003) or because it is more difficult for a pilferer to spy on a hoarder's caching events if these are swift and numerous, as happens with scatter hoarding (reviewed in Dally et al., 2006).

Many field and experimental studies in a variety of systems have shown that food-hoarding animals indeed change their hoarding patterns in response to superior competitors, often by scattering the food items more widely. For example, Merriam's kangaroo rats, *Dipodomys merriami*, change their hoarding patterns in response to cache pilferage by the more aggressive and dominant chisel-toothed kangaroo rat, *Dipodomys microps* (Preston & Jacobs,

2005), and spacing patterns of acorn caches created by wood mice, *Apodemus sylvaticus*, differ between areas with and without wild boar (Muñoz & Bonal, 2007; Puerta-Piñero, Gómez, & Schupp, 2010). No study, however, has yet tested experimentally how cache characteristics resulting from alternative hoarding patterns affect the risk of cache pilferage, while taking into account the hoard size–number trade-off.

We carried out a controlled experiment to determine how hoarding patterns affected the rate at which superior competitors pilfered the hidden food supply. The experiment involved an arena in which we distributed a fixed number of pedunculate oak acorns, *Quercus robur*, over a fixed number of patches, but in varying hoard size–number configurations, ranging from a few caches with many acorns (larder hoarding) to many caches with a single acorn (scatter hoarding). We then measured the rate at which the cached food was pilfered by wild boar, a keen-scented ungulate (e.g. Briedermann, 1986) with a strong preference for acorns (e.g. Focardi, Capizzi, & Monetti, 2000; Groot-Bruinderink, Hazebroek, & Vandervoot, 1994; Herrero, García-Serrano, Couto, Ortuño, & García-González, 2006; Schley & Roper, 2003), which intensely competes for acorns with food-hoarding animals such as wood mice (e.g. Gomez, Garcia, & Zamora, 2003; Muñoz & Bonal, 2007; Perez-Ramos & Maranon, 2008). The interaction between wood mice, wild boar and oaks is interesting, as it is known from previous studies that hoarding patterns of wood mice can vary between individuals and between populations (e.g. Clarke & Kramer, 1994; Den Ouden, Jansen, & Smit, 2005; Jenkins & Breck, 1998; Jennings, 1975; Jensen & Nielsen, 1986; Lu & Zhang, 2005, 2008), and that they can vary depending on wild boar presence (e.g. Focardi et al., 2000; Muñoz & Bonal, 2007; Muñoz, Bonal, & Díaz, 2009; Puerta-Piñero et al., 2010).

We tested contrasting predictions derived from the cue reduction hypothesis and the risk-spreading hypothesis. (1) Scattering is predicted to decrease the rate of pilferage for the first cache(s) and for the last remaining cache(s), because scattered caches emit weaker olfactory cues and are therefore much harder to detect than larders. Thus, the overall rate of pilferage should be lower for scatter hoarding than for larder hoarding (cue reduction hypothesis). (2) Scattering is predicted to increase the rate of pilferage for the first cache(s) because there are simply more caches to be encountered, but to decrease the rate of pilferage for the last remaining cache(s) because it takes more time to encounter many small caches than a few large ones, and therefore the overall rate of pilferage is lower for scatter hoarding than for larder hoarding (risk-spreading hypothesis). To further assess the role of cue reduction in avoiding cache pilferage, we added a scenario in which seeds were buried at greater depth. (3) Pilferage rates are predicted to be lower for deep caches than for shallow ones, owing to weaker olfactory cues emanating from the former (cf. Vander Wall, 1993a).

METHODS

Study System

The wild boar is a medium-sized (50–200 kg) ungulate that is regarded as an important competitor to seed-hoarding rodents in forests and woodlands (Focardi et al., 2000; Gomez et al., 2003). The wild boar is one of the most widespread ungulates in the world. Its natural range extends over most of Europe and Asia and is still expanding rapidly (Massei & Genov, 2004). Female wild boar generally live in family groups of 6–30 individuals, whereas males are mostly solitary (Poteaux et al., 2009). Their natural diet consists of 80–90% plants, but they also feed opportunistically on live and dead animal matter. Being monogastric ungulates, wild boar cannot efficiently extract carbohydrates from cellulose, and therefore rely

on high-energy food items, such as mast of large-seeded trees, and, nowadays, agricultural crops (Groot-Bruinderink et al., 1994; Massei & Genov, 2004; Schley & Roper, 2003). Acorns are a particularly dominant food in autumn when they have been freshly shed and are abundantly available on the forest floor (Elston & Hewitt, 2010; Massei & Genov, 2004), but also in mid- and late winter when very few acorns remain on the forest floor (Den Ouden et al., 2005; Groot-Bruinderink et al., 1994; Muñoz & Bonal, 2007). This suggests that in winter, wild boar actively search for and pilfer acorn caches created by hoarders such as the wood mouse (Borchert, Davis, Michaelsen, & Oyler, 1989; Den Ouden et al., 2005; Focardi et al., 2000; Gomez et al., 2003; Herrera, 1995). Wood mice play an important role as seed predators and dispersers of acorns in Europe. They hoard acorns in autumn as a food reserve for the winter. Food-hoarding patterns of the wood mouse range from almost exclusive scatter hoarding to a mix of scatter- and larder-hoarded caches (e.g. Den Ouden et al., 2005; Lu & Zhang, 2005; Takahashi, Sato, & Washitani, 2007; Vander Wall, 1990). The majority of food items, however, are typically scattered throughout the home range of the wood mouse (e.g. Den Ouden et al., 2005; Jennings, 1975; Jensen & Nielsen, 1986; Shimada, 2001; Suselbeek, Jansen, Prins, & Steele, 2013) with the degree of scattering being larger in the presence of wild boar than in their absence (Puerta-Piñero et al., 2010).

Experimental Procedures and Design

Experimental trials were conducted from 16 February to 25 March 2011, with eight wild boar (five females, three males). Wild boar were taken as 6-month-old piglets from 'Natuurpark Lelystad', The Netherlands, where they had been living with a social group of 12 adult individuals under semiwild conditions in a 7 ha fenced natural area. To capture the wild boar from their living area, a trap of 5 × 5 m was built on 10 August 2010, which had a 0.2 × 0.4 m lockable entrance, to ensure exclusive access for piglets to the trap. The animals were then fed daily in and around the trap to habituate them to it. On 14 September 2010, the animals were fed in the trap at 0700 hours and the entrance was closed during feeding, while eight piglets were inside. A team of five experienced caretakers from the park positioned a wildlife trailer so that the piglets could be swiftly guided through the trap entrance and into the trailer. A prebuilt mobile fence was used to reduce the size of the trap and to direct the piglets (without physical contact) to its entrance and into the trailer. The entire capturing procedure took less than 10 min and was done without administering any drugs to the piglets. The wildlife trailer was not compartmentalized and had an 8 m² floor lined with a 20 cm layer of fresh hay. The trailer was approximately 1.9 m high and had roof hatches at the top of the back door which were all opened to ensure sufficient ventilation during transport. As soon as the animals were in the trailer, they were transported to the experimental facility, a journey that lasted approximately 1 h. Upon arrival, the trailer was again positioned so that the animals could walk out of the trailer without help or physical contact from the caretakers, and into the 1200 m² field enclosure at the experimental facility 'De Haar' in Wageningen, The Netherlands. No adverse effects of capturing and transport were detected. Inside the field enclosure, the wild boar had access to four 8 m² shelter boxes with a layer of fresh hay. The shelter boxes had 1.2 m high walls made of concrete plywood, and a roof covering approximately half of each shelter box. Shelter boxes could be entered by a 0.5 × 1 m opening in the wall at the front and could be entered and exited by the wild boar at all times.

The wild boar had ad libitum access to water and were fed twice daily with fresh and dried plant material supplemented with sow pellets. Every week, a large pile of fresh stems, branches and twigs

was placed in the middle of the field enclosure, below an observation tower, to allow natural sheltering and to provide natural food to the wild boar. Throughout the study, the wild boar were not physically handled, but they were habituated to the presence of the experimenters and the regular caretakers. At the end of the study, the wild boar were culled by a professional wildlife hunter, who is also responsible for the yearly culling of wild boar in 'Natuurpark Lelystad'. All experimental handling procedures were approved by the Animal Experiments Committee of Wageningen University (WUR-2010088.C).

Experimental trials took place in an outdoor arena of 26 × 30 m, consisting of bare clay soil with little or no vegetation. In this arena, a 10 × 10 grid of 100 sand-filled buckets with a diameter of 40 cm were dug into the earth, at regular intervals of 2 m, representing 100 distinct potential cache patches. A 3 m buffer zone was maintained around the grid to avoid edge effects (Fig. 1). Experimental acorns were collected from oaks in the surrounding area and then mixed and stored at low temperatures in large storage trays. Wild boar were habituated to the living area and to the experimental arena for the entire period between arrival (10 September 2010) and the start of experimental trials (16 February 2011). For each trial, a fixed number of 32 experimental acorns was randomly selected from the storage trays, and distributed over the patches. Preliminary results from a complementary field study showed that a density of 32 acorns spread out over an area of approximately 800 m² (i.e. the size of our experimental arena) corresponded well with natural wood mouse hoarding patterns. In this field study, 49 PIT-tagged acorns were offered in 12 different field sites. In each site, 20–40 tagged acorns were relocated after hoarding by wood mice within a radius of 15 m (i.e. an area of 780 m²) around the seed station. This set-up, with a fixed number of acorns distributed over a fixed number of suitable patches within a fixed area, mimics the options available to hoarders for adjusting their hoarding patterns to the risk of pilferage. This level of control would be impossible to achieve in a field study.

We compared three different spacing patterns of 32 acorns over the 100 patches, so as to simulate alternative hoarding patterns: (1) larder hoarding, with two randomly selected patches containing 16 acorns each, (2) intermediate hoarding, with eight patches containing four acorns each and (3) scatter hoarding, with 32 patches containing one acorn each. All caches were created 5–8 cm below the soil surface. These depths approximate the depths reported for seeds hoarded by wood mice (Den Ouden et al., 2005; Jennings, 1975; Mallorie & Flowerdew, 1994). In addition, we ran a fourth treatment ('deep larder hoarding'), in which seeds were larder hoarded as above (treatment 1), but at greater depth: 15–20 cm below the soil surface. All treatments were randomly assigned to trials.

Prior to each trial, soil moisture content (%) was measured (Theta Probe soil moisture sensor ML2x, Delta-T Devices Ltd, U.K.) in three randomly selected patches, with three measurements per patch, as soil moisture is known to affect olfactory cues and with that the detectability of hidden food items (reviewed in Vander Wall, 2003). To avoid potential effects of human scent on cache detection, we wore surgical gloves during all acorn handling, and we raked the soil in all patches prior to each trial, while placing seeds in only some of the patches. At night, and on days without trials, patches were covered with 50 × 50 cm plastic container lids to avoid large fluctuations in soil moisture content within the patches from rainfall. Trials were only conducted in dry weather.

Each trial started with allowing four selected individuals inside the arena to search for the cached acorns. This set-up with four animals simultaneously searching and competing for cached acorns corresponds to the natural situation, where wild boar live and forage together in groups and thus also compete for cached



Figure 1. Overview of the experimental arena and the experimental set-up with sand-filled buckets in which acorns were cached.

resources. During each trial, two observers continuously recorded the order in which all individuals visited the patches in the arena. In addition, all trials were recorded using two video cameras (Panasonic SDR-S50, Panasonic Corp., U.S.A.), positioned so that the entire arena fell inside the combined field of view. Trials ended 2 min after all caches had been found, or when all animals stopped searching for more than 5 min. Trials ended with examination of caches for undiscovered acorns.

The exact timing and order of cache encounter and pilferage were obtained from the combination of observer data and video recordings. The video recordings were prepared for further analysis using a custom-made program modelled in AutoHotkey (Mallet, 2009), which enabled clips from the two cameras to be viewed simultaneously.

Data Analysis

We used Cox proportional hazards (CPH) models (Therneau, 2013) with moisture content as covariate, to test for differences in time until pilferage of the first and the last remaining cache between the alternative hoarding patterns ($N = 16$ for scatter and intermediate hoarding and $N = 15$ for shallow larder and deep larder hoarding). CPH models are frequently used when comparing survival times across treatment levels, as these models can deal well with censored observations and covariates. We included a frailty term (i.e. a random factor, here a unique group identifier) in the survival analysis to account for repeated tests of the same group of wild boar under the same hoarding pattern (Therneau, 2013). We also used CPH models (Therneau, 2013) with moisture content as covariate to test for differences in the overall rate of cache pilferage between the alternative hoarding patterns. All acorn retrieval events from the individual trials were pooled per treatment level, resulting in 512 events for scatter hoarding (32 events \times 16 trials), 128 events for intermediate hoarding (8 events \times 16 trials), and 30 events for both shallow and deep larder hoarding (2 events \times 15 trials). We again included a frailty term (a unique trial identifier) in the survival analysis but this time to account for multiple (non-independent) events within each trial (Therneau, 2013). We used one-sample t tests to compare expected and observed encounter probabilities of caches across treatment levels. Expected encounter probabilities were defined based on the ratio of empty patches to

cache patches, for each hoarding pattern. For example, in the case of scatter hoarding, 32 of 100 available patches contained a cache, resulting in a 32% probability that a randomly encountered patch contained a cache. Thus, these were fixed probabilities for each treatment level (i.e. 0.32 for scatter hoarding, 0.08 for intermediate hoarding and 0.02 for larder hoarding). These expected encounter probabilities were then compared to the true observed encounter probabilities, which were based on the actual ratio of empty patch to cache patch visits by one prior-defined focal individual for each trial. Group composition may influence the response of the focal individual; however, since we had repeated measurements for the same focal individual in groups composed of different individuals, we first averaged the observed visit rates for each individual and then used these in the analysis. All analyses were carried out in R 2.12.2 (R Development Core Team, 2011).

RESULTS

A total of 62 trials were run, with 21 replicate groups of wild boar (i.e. groups that consisted of a unique combination of individual wild boar). Altogether, 16 trials (12 replicate groups tested) were run for scatter hoarding, 16 trials (11 replicate groups tested) for intermediate hoarding, 15 trials (11 replicate groups tested) for shallow larder hoarding and 15 trials (15 replicate groups tested) for deep larder hoarding. See Appendix Tables A1 and A2, respectively, for summaries of (1) the number of times that each wild boar was tested within each treatment level and (2) the number of times that each group of wild boar was tested within each treatment level. Soil moisture content ranged between trials from 1.6% to 7.2% (mean 4.2%, $SD = 1.3$), but did not differ between treatments (one-way ANOVA: $F_{3,58} = 0.19$, $P = 0.9$).

Hoarding pattern significantly influenced the time it took a group of wild boar to pilfer the first cache (Cox proportional hazards model: Wald $\chi^2 = 21.0$, $P < 0.001$; Fig. 2a) and the last remaining cache of a trial (Cox proportional hazards model: Wald $\chi^2 = 16.5$, $P = 0.003$; Fig. 2b). In line with our second prediction, the time until pilferage of the first cache was significantly shorter under scatter hoarding (mean = 6.2 s, 95% CI = 4.6–8.5) than under intermediate (12.9 s, 8.2–20.4) or larder hoarding (41.0 s, 19.7–85.0), whereas pilferage of the last remaining cache took significantly more time under scatter hoarding (mean = 567 s, 95%

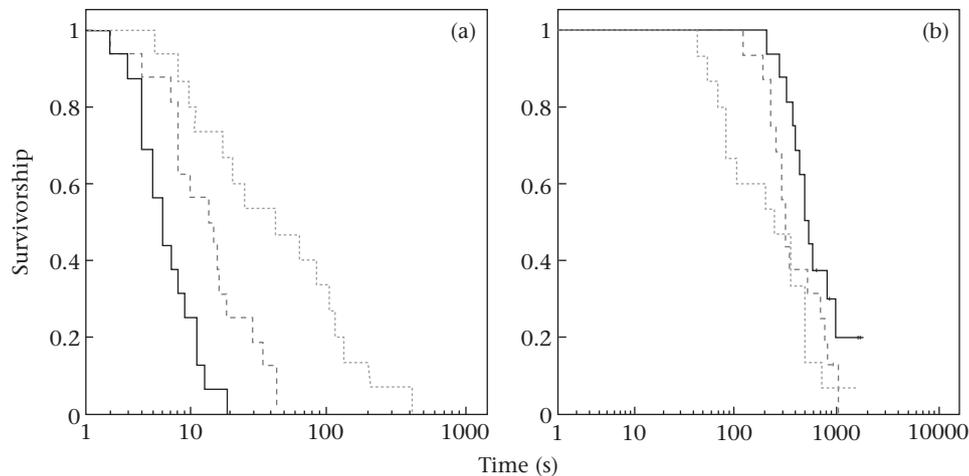


Figure 2. Effect of hoarding pattern on the rate of cache pilferage by wild boar in a controlled experiment. Survivorship curves indicating time to pilferage for (a) the first cache and (b) the last remaining cache, for scatter hoarding (solid line), intermediate hoarding (dashed line) and larder hoarding (dotted line). Crosses in curves represent censored observations.

CI = 415–774) than under intermediate (389 s, 278–545) or larder hoarding (221 s, 122–400). Soil moisture content did not explain any variation in the time it took to pilfer the first cache (Wald $\chi^2 = 0.6$, $P = 0.44$); however, regardless of the hoarding pattern, an increase in soil moisture content reduced the time it took a group of wild boar to pilfer the last remaining cache (Wald $\chi^2 = 10.0$, $P = 0.002$).

Contrary to our predictions, hoarding pattern did not affect the overall rate at which acorns were pilfered by a group of wild boar (Cox proportional hazards model: Wald $\chi^2 = 9.1$, $P = 0.996$; Fig. 3a). The average proportion of caches pilfered after 5 min of wild boar searching did not differ between scatter hoarding (86.5%, $N = 16$) and larder hoarding (73.3%, $N = 15$; Mann–Whitney U test: $U = 114$, $P = 0.81$) and the probability that all caches had been pilfered after 10 min of searching also did not differ significantly between scatter hoarding (62.5%, $N = 16$) and larder hoarding (86.7%, $N = 15$; Pearson $\chi^2 = 2.36$, $P = 0.12$). Regardless of the hoarding pattern, the overall rate of pilferage increased significantly with soil moisture content (Wald $\chi^2 = 7.5$, $P = 0.006$).

Contrary to our third prediction, cache depth did not influence the overall rate of cache pilferage by wild boar (Wald $\chi^2 = 0$, $P = 0.988$; Fig. 3b). Cache depth also did not affect the time it took a

group of wild boar to pilfer the first cache (Wald $\chi^2 = 0.12$, $P = 0.73$; Fig. 4a) or the last remaining cache (Wald $\chi^2 = 0.06$, $P = 0.81$; Fig. 4b).

These results suggest that wild boar visited patches more or less randomly, regardless of whether they contained a cache. We verified this possibility by comparing the random encounter probability of patches that contained acorns with the observed encounter rate of such patches. Observed encounter rates for patches that contained a cache did not differ from expected encounter rates based on random patch visits, irrespective of the hoarding pattern (one-sample t tests: all P values > 0.05 ; Table 1).

DISCUSSION

We conducted a controlled experiment to determine how alternative hoarding patterns influenced pilferage of cached acorns by a large nonhoarding food competitor, the wild boar. We found that scatter hoarding, as expected, reduced survival time for the first cache and slightly increased survival time for the last remaining cache. The overall rate of pilferage by wild boar did not, however, differ between scatter and larder hoarding, and the overall rate of pilferage was also not influenced by cache depth. This

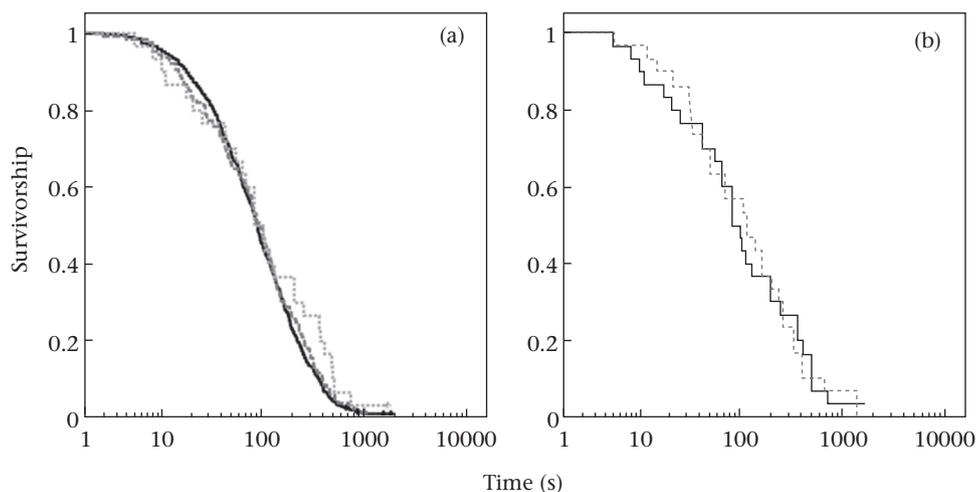


Figure 3. Effects of hoarding pattern and cache depth on the overall rate of acorn pilferage by wild boar for all trials, pooled per treatment. (a) Survivorship curves for scatter hoarding (solid line), intermediate hoarding (dashed line) and larder hoarding (dotted line). (b) Survivorship curves for shallow larder hoarding (solid line) and deep larder hoarding (dashed line). Crosses in curves represent censored observations.

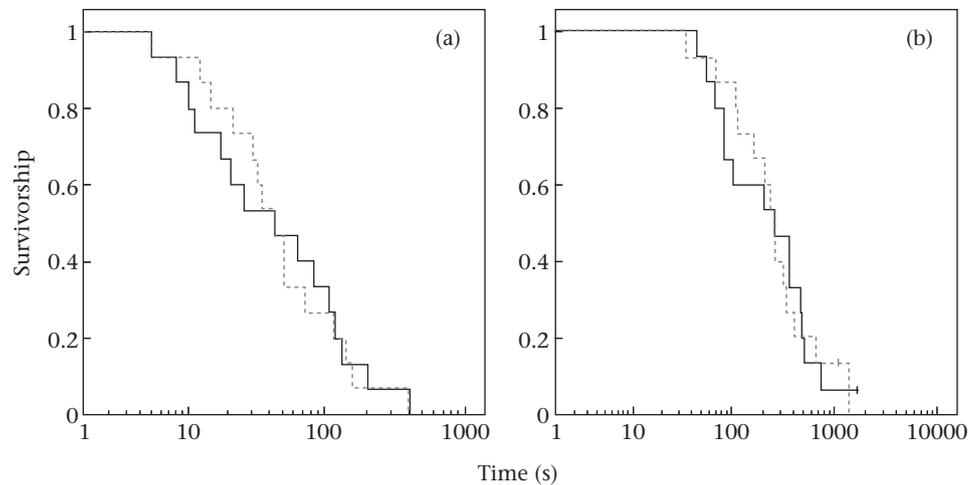


Figure 4. Effect of cache depth on the rate of cache pilferage by wild boar in a controlled experiment. Survivorship curves indicating time to pilferage for (a) the first cache and (b) the last remaining cache, for shallow larder hoarding (solid line) and deep larder hoarding (dashed line). Crosses in curves represent censored observations.

suggests that wild boar were either unable to pick up olfactory cues from acorn caches, for example because these were too weak, or that wild boar were not using olfactory cues to locate cached acorns.

Our finding that scatter hoarding increased the rate of pilferage of the first cache(s), but reduced the rate of pilferage of the last remaining cache(s) is in agreement with the risk-spreading hypothesis. This hypothesis argues that scattering of food increases the probability of a pilferer randomly encountering some caches (as simply more patches contain a cache) but that it also increases the effort needed to locate all caches. As a consequence, the probability of at least some caches escaping pilferage is assumed to be higher (Dally et al., 2006; Devenport et al., 2000; Jacobs, 1992; Kraus, 1983; Macdonald, 1997). These findings are not, however, in line with the cue reduction hypothesis, under which scatter hoarding should reduce the rate of pilferage for both the first and the last remaining cache(s) as weaker olfactory cues emanate from scatter hoards than larder hoards (as a consequence of scatters being smaller; e.g. Geluso, 2005; Reichman & Oberstein, 1977; Vander Wall, 1993a, 1998, 2003). Furthermore, we found no effect of cache depth on pilferage by wild boar, even though several studies have shown that shallow caches emanate stronger olfactory cues than deep ones (reviewed in Vander Wall, 2003). This, together with the results of the comparison between expected and observed cache encounter probabilities, suggests that cue reduction is not the mechanism whereby rodents avoid pilferage by wild boar. This could be because olfactory cues emanating from acorn caches were too weak to be picked up by wild boar, or because wild boar locate caches by systematic searches rather than by the use of olfactory cues.

The finding that wild boar may not be able to pick up olfactory cues from buried acorns or may not be using them for cache finding was unexpected, as wild boar are well-known for their sensitive

olfactory senses. Much of the literature's acclaim of the wild boar's sense of smell is, however, based on their capacity to locate black truffles (see Briedermann, 1986). Black truffles and all other hypogeous fungi have evolved to produce their fruiting bodies below ground and thus they rely, for having their spores dispersed, on being found and dug up by animals (e.g. Bellina-Agostinone, D'Antonio, & Pacioni, 1987; Bruns, Fogel, White, & Palmer, 1989; Johnson, 1996; Pyare & Longland, 2001; Talou, Gaset, Delmas, Kulifaj, & Montant, 1990). Acorns, by contrast, are the fruiting bodies of oak trees that require transport by scatter-hoarding animals to reach a location for germination and establishment, and so it is unlikely that there has been a selective advantage for oaks to produce acorns that can be found and destroyed by wild boar. On the contrary, selection pressure may have favoured acorns that emanate weak olfactory cues that cannot be picked up efficiently by seed predators such as the wild boar. Consequently, wild boar may only be able to locate cached acorns easily by opportunistically foraging and rooting at locations likely to have acorns, such as directly below and around adult oak trees. This would also provide an explanation for high concentrations of rooting found below and directly around these trees (e.g. Groot-Bruinderink & Hazebroek, 1996; Welander, 2000). If wild boar were able to pinpoint the location of cached acorns by means of olfaction, one would expect to see many small rooting patches rather than a few large ones. Nevertheless, a useful follow-up experiment would be to focus on the wild boar's ability to detect (hidden) acorns on the basis of olfaction, and perhaps to test at which spatial scale these olfactory cues could be picked up.

Pilferage rates of cached acorns by wild boar did not differ between scatter and larder hoarding. The question thus arises: why do many animals primarily scatter hoard their food items? First, and perhaps most importantly, scatter hoarding is assumed (and

Table 1

One-sample *t* test results of the comparison between mean observed and mean expected cache encounter probabilities for eight individual wild boar

Treatment	Mean expected	Mean observed	Median observed	<i>t</i> (<i>df</i>)	<i>P</i>	95% CI
Scatter (32 caches)	0.320	0.309	0.319	−0.634 (7)	0.55	0.269–0.350
Intermediate (8 caches)	0.080	0.074	0.077	−1.036 (7)	0.33	0.059–0.088
Shallow larder (2 caches)	0.020	0.029	0.030	0.949 (7)	0.37	0.007–0.051
Deep larder (2 caches)	0.020	0.029	0.026	0.871 (7)	0.41	0.005–0.053

was found in our study) to be a strategy to lower the risk of a catastrophic loss (i.e. instantaneously losing the entire food supply; e.g. Dally et al., 2006; Smith & Reichman, 1984; Vander Wall, 1990). Although several studies have suggested that complete pilferage by superior competitors poses the largest threat of catastrophic loss (e.g. Macdonald, 1997; Preston & Jacobs, 2001; Zhang, Wang, & Zhang, 2011), there may be several other factors that could result in such a loss. For example, many large seeds are prone to fungal infections owing to their high natural moisture content. Caching large quantities of such seeds together may thus pose a large threat of catastrophic loss from fungal cross-contamination (e.g. Edelman, 2011; Reichman, Wicklow, & Rebar, 1985). Similarly, physical disturbance of the cache (through e.g. windthrow) as well as density-responsive seed predators (Janzen, 1970) may pose a large threat of catastrophic loss. Another possibility is that scatter hoarding by wood mice is a response to competition with conspecifics and that hoarding patterns depend on the individual characteristics of the hoarder, in terms of its dominance over conspecific competitors (Clarke & Kramer, 1994), a response that has also been shown for other species (e.g. Daly et al., 1992; Leaver, 2004; Preston & Jacobs, 2001; Sanchez & Reichman, 1987; Zhang et al., 2011). Finally, although scatter hoarding does not seem to have a large effect on pilferage risk by wild boar, this effect may be different for other species, depending on the cues provided by the caches and by the hoarder itself, and depending on the search tactics applied by the pilferer. For instance, hedgehogs, *Erinaceus europaeus*, and red foxes, *Vulpes vulpes*, which use olfaction to locate buried eggs, have been shown to be able to detect (by smell) eggs buried at 3 cm depth up to a distance of 50 cm and 3 m, respectively (Tinbergen, 1965). After retrieval of a buried egg, hedgehogs only searched in an approximately 1 m² area around the cache location, suggesting that scattering individual food items beyond the olfactory detection distance of the pilferer reduces pilferage risk.

One aspect that should not be overlooked here is the direct risk of predation imposed upon wood mice by wild boar. Wild boar are known to have a very diverse diet, which certainly includes animal matter, ranging from insects and worms to mice and voles, and they even scavenge around the carcasses of larger animals (Briedermann, 1986). It is thus not unlikely that wild boar form a direct threat to the survival of wood mice, and as a consequence, wood mice might have adjusted their hoarding patterns so that the risk of predation by wild boar, rather than the risk of pilferage, is minimized (Focardi et al., 2000; Muñoz & Bonal, 2007; Puerta-Piñero et al., 2010). Generally, larder hoards are connected to the underground burrow system of the hoarder and are usually located near the hoarder's nest, whereas scatter hoards are created from the soil surface, and are usually not connected to the burrow system of the hoarder (Jennings, 1975; Vander Wall, 1990). The scatter-hoarding set-up, where food is detached from the burrow system, is likely to reduce the risk of wild boar encountering the nest or hiding place of a hoarder while it is searching for buried food items (Vander Wall, 1990, 2001).

Our experiment, in which we distributed a fixed number of acorns over a fixed number of potential cache locations within a fixed area, was designed to mimic alternative outcomes of the hoard size–number trade-off that hoarders face. Given a certain food supply (i.e. a fixed number of seeds or other food items) and available area (i.e. the home range), pilferage rates can be influenced only by changing the distribution of food items over the available patches and by varying the depth at which food items are cached. In our experiment, we controlled for the number of food items and the number of available patches as well as for pilferer pressure (i.e. the number of wild boar in the area). Nevertheless, two aspects of our study differ slightly from the natural situation:

(1) we used a fixed number of distinct patches, rather than a continuous area in which caches could be created and (2) wild boar could have been aware that hidden food items were present in the experimental arena during each trial. These aspects may have facilitated exploration by wild boar and may thus have inflated the rate with which caches were pilfered, compared with a truly natural situation. Since these conditions were similar across different treatments, however, this will not have influenced our final conclusion. Finally, in a natural situation, wild boar may be using cues other than those assumed in this study. For instance, they may use visual or olfactory cues to locate the entrance of a hoarder's burrow system and accordingly uproot the entire system (Focardi et al., 2000). If this were true, it would particularly favour scatter hoarding.

The results from this study suggest that the overall rate of pilferage by wild boar is little affected by the hoarding pattern applied by the food hoarder. This would suggest that superior competitors are not driving the decision of a hoarder to scatter hoard. Nevertheless, scatter hoarding may have the potential to lower the risk of catastrophic loss of food reserves, but the extent to which it does so probably depends on the cues provided by the caches and by the hoarder, and on the search tactics used by the pilferer. Finally, there may be other factors, such as conspecific pilferage, physical cache disturbance or cross-contamination of food items, that could also lead to catastrophic loss of food reserves and as such could be important drivers of the decision of animals to scatter hoard the majority of their food reserves.

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APPENDIX

Table A1

Summary of the number of times that each of the eight individual wild boar was part of a team that was tested in each of the four treatment levels

		Scatter hoarding	Inter-mediate hoarding	Shallow larder hoarding	Deep larder hoarding
1	F1_ALF	5	6	6	6
2	F2_BIL	8	8	7	9
3	F3_MAT	6	6	6	7
4	F4_OSW	7	6	6	3
5	F5_SOP	9	11	10	8
6	M1_BIG	10	10	10	10
7	M2_CHA	8	7	6	7
8	M3_HAZ	11	10	9	10
	Total	64	64	60	60

Column totals represent the total number of individuals tested in each treatment level (e.g. there were 16 trials with four individuals for the scatter-hoarding treatment, resulting in a total of 64 individuals tested in this treatment level).

Table A2

Summary of the number of times that each of the 21 unique groups of wild boar was tested within each of the four treatment levels

					Scatter hoarding	Inter-mediate hoarding	Shallow larder hoarding	Deep larder hoarding
1	F1_ALF	M1_BIG	F2_BIL	M2_CHA				1
2	F1_ALF	M1_BIG	F2_BIL	M3_HAZ	1	1	1	1
3	F1_ALF	M1_BIG	F2_BIL	F5_SOP		1		
4	F1_ALF	M1_BIG	M2_CHA	M3_HAZ	1	1	1	1
5	F1_ALF	M1_BIG	M3_HAZ	F5_SOP			1	
6	F1_ALF	F2_BIL	F3_MAT	F5_SOP				1
7	F1_ALF	M2_CHA	M3_HAZ	F3_MAT				1
8	F1_ALF	F3_MAT	F4_OSW	F5_SOP	3	3	3	1
9	M1_BIG	F2_BIL	M2_CHA	M3_HAZ	3	2	2	1
10	M1_BIG	F2_BIL	M2_CHA	F5_SOP			1	
11	M1_BIG	F2_BIL	M3_HAZ	F3_MAT				1
12	M1_BIG	F2_BIL	M3_HAZ	F5_SOP	1	1	1	1
13	M1_BIG	F2_BIL	F3_MAT	F5_SOP				1
14	M1_BIG	F2_BIL	F4_OSW	F5_SOP	1			
15	M1_BIG	M2_CHA	M3_HAZ	F3_MAT	1	1	1	1
16	M1_BIG	M2_CHA	M3_HAZ	F5_SOP	1	2	1	1
17	M1_BIG	M3_HAZ	F4_OSW	F5_SOP	1	1	1	1
18	F2_BIL	M2_CHA	M3_HAZ	F4_OSW	1			
19	F2_BIL	M2_CHA	M3_HAZ	F5_SOP		1		1
20	F2_BIL	F3_MAT	F4_OSW	F5_SOP	1	2	2	1
21	M2_CHA	M3_HAZ	F3_MAT	F5_SOP	1			
	Total				16	16	15	15

Column totals represent the total number of trials for each treatment level (e.g. there were 16 trials for the scatter-hoarding treatment).