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Reciprocal pilferage and the evolution of food-hoarding behavior

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Current theories of food-hoarding behavior maintain that hoarding can be adaptive if a hoarder is more likely than any other animal to retrieve its own caches. A survey of the literature indicated that the hoarder often has a recovery advantage when searching for items it has stored, but levels of cache pilferage are often so high (2–30% per day) that at least for some long-term food hoarders, the caching animal is unlikely to recover a significant amount of its stored food. Except in a few cases (acorn woodpeckers and beavers), kin selection cannot explain the high levels of pilferage observed. We suggest that some small solitary animals with overlapping home ranges (e.g., most rodents, chickadees, and tits) are able to tolerate high levels of cache pilferage. Pilferage is not as damaging to these animals as it might otherwise be because many interspecific and all intraspecific cache pilferers also cache food. These or similar food caches can be pilfered later by the original food hoarder. In other words, pilfering in these species is often reciprocal, and because it is reciprocal, it can be tolerated. We argue that caching systems based on reciprocal pilfering can be stable and are not necessarily susceptible to "cheaters," animals that pilfer food but do not scatter hoard food themselves, and we introduce a model of food hoarding to support this argument. These food-caching systems based on reciprocal pilfering resemble cooperative behavior, but the behavior is actually driven by the selfish interests of individuals. This theory of scatter-hoarding behavior based on reciprocity has important implications for the ways that food-hoarding animals interact with inter- and intraspecific competitors. *Key words:* cheating, food caching, granivory, kin selection, larder hoarding, olfaction, pilferage, reciprocity, recovery advantage, scatter hoarding, spatial memory. *[Behav Ecol 14:656–667 (2003)]*

Since the late 1970s, a theory of scatter-hoarding behavior has emerged based on the assumption that for scatter hoarding to be profitable for the hoarder, the hoarder must retrieve a sufficient proportion of the food it has stored to repay its effort. Models developed and tested by Stapanian and Smith (1978, 1984), Clarkson et al. (1986), and others to explain spatial patterns of scatter hoarding were based on the premise that the value of cached food to the hoarder is equal to the ability of the hoarder to retrieve those items. Andersson and Krebs (1978) developed a model of hoarding behavior, and they concluded that hoarding can be adaptive "if a hoarder is more likely than any other group member to retrieve *its own items* [italics added]." An important focal point of these models was the occurrence of pilfering, the removal of cached food items by an individual other than the cacher, and its potentially deleterious effect on the evolution of hoarding behavior. It is generally believed that for food hoarding to evolve, animals must keep pilferage to some acceptably low level. To achieve this, food-hoarding animals must have evolved behavioral and spatial patterns of hoarding that minimized pilferage. Food-hoarding animals that cannot defend large concentrations of stored food (larders) are compelled to space food items widely and hide them carefully (i.e., scatter hoarding) so they cannot easily be found by other animals.

Considerable effort has been invested in understanding how food-hoarding animals control pilferage of stored items (see Clarke and Kramer, 1994b; Daly et al., 1992; Ekman et al., 1996; Stevens and Krebs, 1986). Not all of the data gathered are consistent with the notion that scatter-hoarding animals are capable of keeping pilferage to a low level. For example, Kraus (1983) found that rodents pilfered more than 95% of 218 artificially cached walnuts in 24 h. The above-cited models of the evolution of scatter-hoarding behavior do not seem compatible with such high levels of cache pilferage. The purpose of this article is to review data relevant to the existing theory of the evolution of hoarding behavior. We will show that certain aspects of the current theory have little empirical support. We will then present an alternative view for the evolution of hoarding behavior based on the theory of reciprocity.

Pilferage of scatter-hoarded food

Long-term hoarders are those that cache food over a seasonal cycle, usually to be consumed months later. Short-term hoarding, on the other hand, occurs over one or several days, often in the context of daily energy or body mass management (Lucas and Walter, 1991; McNamara et al., 1990; Pravosudov and Grubb, 1997a,b). Because of the time scale, pilferage at any rate will have less effect on short-term hoarders than on long-term hoarders. For example, rates of pilferage in the range of 2–10% per day are likely to have little effect on an individual that stores food for less than 3 days, but cache loss at this rate could have catastrophic effects on an animal that stores food for several months (Figure 1).

Ecologists have conducted dozens of field studies on the rates of disappearance of artificial caches. Such studies are informative because any removal must be attributed to pilferers. These studies usually involve establishing an array of buried or hidden food items in the manner of a specific food hoarder. These arrays are then monitored over time to document loss of items. We summarize many of these studies in Table 1.

Most pilferage rates for long-term hoarders fall between 2–30% per day! If these artificial caches accurately represent the fates of real caches, then the food stores of these animals would be depleted within one to several weeks. The pilferage

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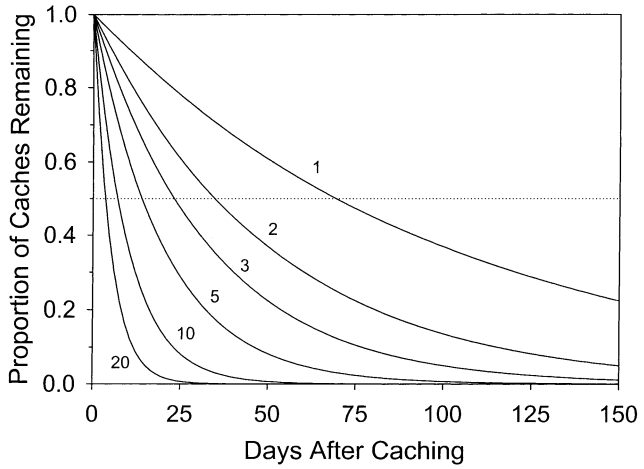


Figure 1
Hypothetical rates of cache pilferage (loss) for a population of caches over a period of 150 days. Numbers along curves are percentages of caches removed per day.

rates for short-term hoarders are higher than those for long-term hoarders (usually 5–60% per day) (Table 1), but because these animals retrieve cached items within hours or days of caching, these high rates of pilferage may have less impact on the stored food supply.

There is some need for concern over whether these artificial caches accurately reflect the fates of real caches. Experimenters have used flagging or map pins to mark cache sites (Cowie et al., 1981; Kraus, 1983; Sherry et al., 1982), have wrapped nuts in aluminum foil or paper (Rice-Oxley, 1993; Stapanian and Smith, 1978, 1984), or have placed seeds in plastic dishes buried in the ground (Daly et al., 1992). Foragers may have learned to recognize these cues and used them to remove hidden items much more rapidly than they could have otherwise. However, these potential cues seem unlikely to provide a complete explanation for the high rates of removal for several reasons. First, most experimenters were aware of this possibility and took great care to minimize the chance that cache markers could have been used as cues. For example, markers were usually placed well away from cache sites (see Kraus, 1983; Sherry et al., 1982), and many "false" markers were placed around the cache arrays where no caches were made so that markers did not always provide useful information to foragers (see Bardin and Markovets, 1991; Kraus, 1983). Second, several of the studies reported in Table 1 used no markers at all and still showed high levels of cache pilferage. Henry (1986), Waite (1988), and Verbeek (1997) relied on detailed notes to relocate cache sites; James and Verbeek (1983) and Pyare and Longland (2000) used a measuring tape to return to caches; and one of us (Vander Wall 1998) used radioactive isotopes and a Geiger counter to find cache sites. Rates of pilferage in these studies usually ranged from about 2–36% per day. Finally, pilferage of artificial caches appears to occur at rates comparable to those documented in studies of natural caches (see Brodin, 1993; Clarke and Kramer, 1994a; Daly et al., 1992; James and Verbeek, 1985).

The effect of cache spacing

Cache spacing is thought to be one of the means by which scatter-hoarding animals protect cached food from pilferers (Clarkson et al., 1986; Daly et al., 1992; Sherry et al., 1982; Stapanian and Smith, 1978, 1984). By spacing cached items widely, food hoarders discourage area-restricted search by naive competitors that may happen to discover a buried item. Generally, the hypothesis that greater spacing reduces pilferage has been supported (Daly et al., 1992; Sherry et al., 1982; Stapanian and Smith, 1978, 1984; Tamura, 1999; Waite, 1988), but Kraus (1983) and Henry (1986) found that rates of pilferage were not correlated with cache density. However, even when the predictions of the optimal cache-spacing hypothesis are upheld, pilferage rates are unexpectedly high. Ecologically relevant spacings in these studies resulted in removal rates of 1.5–27.6% per day for long-term hoarders and 3.0–26.0% per day for short-term hoarders (Table 1).

It appears, as Kraus (1983) has suggested, that the effect of spacing stored food is to reduce the rate of pilferage, not eliminate it altogether. The behavior of scatter-hoarding animals suggests that they are aware of and respond to spatial variation in cache density, and they attempt to keep cache density below a certain level (Vander Wall, 1995b; Waite and Reeve, 1995). Dense concentrations of stored food can occur around a feeder or other rich source, but animals treat these concentrated stores differently from other cached items (Bardin and Markovets, 1991; Brodin, 1994b); they quickly retrieve and recache the food at more distant sites (Bardin and Markovets, 1991; Jokinen and Suhonen, 1995; Waite and Reeve, 1995). It is clear from these and other studies that cache density is important, but simply spacing caches widely is apparently insufficient to eliminate pilfering.

Kin selection and evolution of hoarding behavior

Perhaps high rates of pilferage among group-living animals are not a problem for the theory of scatter hoarding because most pilferers are close kin of the hoarder. If this is true, pilfered caches could contribute to inclusive fitness of the hoarder through kin selection, compensating for possible losses to the individual component of fitness. There are only two species in which kin selection appears to have resulted in sharing of food stores within the social group. Acorn woodpeckers (*Melanerpes formicivorus*) are unusual in that they construct a conspicuous communal larder (Koenig and Mumme, 1987). Beavers (*Castor canadensis*) live in family groups and construct winter larders of submerged branches. It appears that adults construct these caches largely for the benefit of kits and yearlings (Novakowski, 1967).

A number of jays live in family groups, but sharing of cached food has not been demonstrated (see DeGange et al., 1989; Ekman et al., 1996; Stotz and Balda, 1995). In fact, group members appear to act selfishly, caching and retrieving items secretively (Waite, 1992). Most other species of food-hoarding animals do not live in kin groups, even though natal dispersal is often less than 200 m (see Jones, 1993). Nearly all food-hoarding rodents (e.g., kangaroo rats, chipmunks, squirrels) do not maintain family groups after the reproductive season, and food caching is a solitary endeavor (Elliott, 1978; Jones, 1993; Stapanian and Smith, 1978). The young of tits and chickadees disperse during summer, so winter flocks consist of unrelated individuals (Ekman, 1979, 1989; Moreno et al., 1981; Smith, 1991). Furthermore, birds appear to behave selfishly when storing and recovering food (James and Verbeek, 1983; Källander, 1978; Härdling et al., 1995; Heinrich and Pepper, 1998; Stone and Baker, 1989) and are often hesitant to store food while being watched by conspecifics (Alatalo and Carlson, 1987; Carrascal and Moreno, 1993; Lahti and Rytkonen, 1996).

The clearest examples of sharing of stored food occur between parents and dependent offspring, but even this is curtailed as young mature. For example, female eastern chipmunks (*Tamias striatus*) often move food out of their burrows late in the reproductive season to avoid pilferage of

Table 1
A survey of pilferage from artificial caches

Species simulated	Food type	Spacing (m)	Depth (cm)	Duration of test (day)	Rate of pilferage: No. taken/ no. present	Rate of pilferage: Percentage per day	Reference
Studies of long-term scatter hoarding							
Sciurus niger	black walnuts	2.4 grid	2–4	21	60–61/64	8.5–9.4	Stapanian and Smith, 1978
		4.6 grid	2–4	21	50–53/64	4.8–5.5	
		9.2 grid	2–4	21	8–35/64	0.4–2.5	
	acorns and black walnuts	variable	1–2	6	22/49–45/49	9.4–33.2	Stapanian and Smith, 1984
Sciurus carolinensis	horse chestnuts	variable	0.5	188	423/500	1.0	Thompson and Thompson, 1980
	California walnuts	2–8 grid	2–4	3	25/25	>95	Kraus, 1983
Sciurus vulgaris	peanuts	variable	2.4	1	≈9–24/25	36–96	Rice-Oxley, 1993
Sciurus lis	Japanese walnuts	1 (<30m)*	covered	3	10.4/20	21.7	Tamura et al., 1999
		1 (<30m)*	covered	9	14.1/20	12.7	
		1 (>30m)*	covered	3	4.1/20	7.4	
		1 (>30m)*	covered	9	6.9/20	4.6	
Tamias amoenus	Jeffery pine seeds	variable dry	0.5	3	7/240	1.0	Vander Wall, 2000
		variable wet	0.5	3	273/424	29.1	
P. maniculatus	Jeffery pine seeds	variable dry	0.5	3	7/240	1.0	
		variable wet	0.5	3	238/424	24.0	
Tamias amoenus	Jeffery pine seeds	4.0	0.5	5	35/80	7.5	Vander Wall and Peterson, 1996
		4.0	0.5	5	17–19/80	4.7–5.3	
Garrulus glandarius	acorns	0.5 line	0.5	30	94/100	9.0	Bossema, 1979
		0.5 line	0.5	19	202/360	4.2	
Perisoreus canadensis	raisins	2.12/m^3	hidden	10	40/40	>36.0	Waite, 1988
		0.24/m^3	hidden	10	37/40	22.8	
		0.06/m^3	hidden	10	31/40	13.8	
Parus montanus	sunflower and juniper	variable	hidden	126	20/100	1.3	Brodin, 1993
	sunflower	variable	hidden	10	11/100	1.3	
Parus spp.	sunflower	≈2	hidden	30	≈1119/1138	12.8	Bardin and Markovets, 1991
		≈2	hidden	first 5	1025/1138	37.0	
		≈2	hidden	last 25	94/113	6.9	
Dipodomys spp.	Indian ricegrass	variable	3	7	27/30	28.0	Pyare and Longland, 2000
Studies of short-term scatter hoarding							
Parus palustris	sunflower	1.0	hidden	≈4	21/30	≈26.0	Cowie et al., 1981
		1.8	hidden	1	14.4/25	57.6	Sherry et al., 1982
		3.6	hidden	1	16.6/25	66.4	
		7.2	hidden	1	9.5/25	38.0	
		10.8	hidden	1	9.7/25	38.8	
		14.4	hidden	1	6.9/25	27.6	
Corvus caurinus	clams	variable	covered	8	91/106	21.7	James and Verbeek, 1983
		variable	covered	<1	8/111	>7.2	James and Verbeek, 1985
		1.0 paired	covered	<1	10/50	>20.0	Verbeek, 1997
Vulpes vulpes	dog food	2.75 grid	12.5	7	30/135	3.5	Henry, 1986
		13.7 grid	12.5	7	41/135	5.0	
		68.6 grid	12.5	7	26/135	3.0	
Dipodomys merriami	millet	.25–.50	1	1	61/120	51.0	Daly et al., 1992
		1–2	1	1	48/120	40.0	
		4–8	1	1	31/120	26.0	
Tamias striatus	sunflower	variable	1–3	<1	18/18, 18/18	100.0	Clarke and Kramer, 1994a

Because researchers used different methods and reported removal of caches in different ways, we use their data to estimate a common statistic: daily rates of removal of cached items. Calculations are based on the assumption that the rate of removal over the duration of a study was constant.

* Artificial caches were made either <30 m or >30 m from a concentrated food source.

food by their own young (Clarke and Kramer, 1994a). There are rare instances in which animals do share stored food. Wintering taiga voles (*Microtus xanthognathus*) construct and feed from a communal larder. This behavior may have evolved as a means of conserving body heat by communal huddling, but the sharing of the larder cannot be explained by kin selection because most members of the group are not related (Wolff and Lidicker, 1981).

In summary, kin selection appears to have played an important role in the evolution of communal use of stored food only in acorn woodpeckers and beavers. In several species of group-living jays, kin selection may eventually prove to have been important in the evolution of hoarding behavior, but this has not been demonstrated and available evidence suggests that hoarding behavior has been shaped by individual selection.

Advantages of the cacher over pilferers

It is generally believed that for food hoarding to evolve and persist the food hoarder must have an advantage over pilferers when foraging for its caches (Andersson and Krebs, 1978; Stapanian and Smith, 1978; but see Smulders, 1998). Food-hoarding animals appear to achieve this advantage in three ways: (1) aggressive behavior to restrict access to areas used for caching, (2) spatial memory of inconspicuous cache sites, and (3) use of different caching and foraging microsites within social groups. Most food-hoarding animals use two or more of these to improve their chances of retrieving the food they store.

Aggression

Animals can exclude potential competitors from their territory or area around their burrow to lower the probability of pilfering (Clarke and Kramer, 1994a; DeGange et al., 1989; Härdling et al., 1995; Jones, 1993; Moreno et al., 1981; Woodrey, 1991). For example, flocks of tits and chickadees exclude other parids from their winter territories, where they have hidden thousands of food items (Brodin, 1994b; Ekman, 1979, 1989; Lens et al., 1994; Smith, 1991). Within these stable winter flocks, the adult male typically dominates other flock members, excluding them from his favored foraging and hoarding microhabitat (Baker et al., 1990; Brodin, 1994b; Ekman, 1979).

Aggressive defense of stored food seems essential for most larder hoarders. Studies on the effects of cache spacing on rates of pilferage have found that the variance in cache loss increases as the distance between caches decreases, and is greatest when all of the food is placed together (i.e., in a larder; Daly et al., 1992; Henry, 1986). These data suggest that if a larder is not defended, when pilferage occurs it is likely to be very detrimental to the hoarder. Species as diverse as red squirrels (*Tamiasciurus hudsonicus*), Merriam's kangaroo rats (*Dipodomys merriami*), eastern chipmunks, and acorn woodpeckers all aggressively defend larders from conspecifics. Some species establish larders because it is the most economical way to manage and retrieve their food stores (e.g., pikas, *Ochotona princeps*; acorn woodpeckers; red squirrels). However, other species seem forced to larder hoard. For example, the pilferage rate of eastern chipmunk caches (Clarke and Kramer, 1994a; Table 1) is so high that over the long term, the food hoarder has only a small chance of retrieving a food item if it is scatter-hoarded. To ensure the long-term availability of stored food, eastern chipmunks must place the food in a larder that they aggressively defend.

Spatial memory

Knowledge of cache locations is unique to the hoarder (unless it is observed in the act of caching) and gives the hoarder a marked advantage in recovering hidden food. Since 1980, a wealth of data have been collected that demonstrate the impressive spatial memories of food-storing birds (see Hitchcock and Sherry, 1990; Kamil and Balda, 1985; Sherry et al., 1981; Shettleworth and Krebs, 1982; Vander Wall, 1982). Spatial memory is especially important in cache recovery for jays and nutcrackers (*Nucifraga*) that bury seeds in soil because the seeds are very well hidden and, even though they emit weak odors, birds have virtually no sense of smell for seeds. Intraspecific cache pilferage is usually low in these species. Spatial memory may be less critical to birds that store food in foliage and bark (e.g., tits, nuthatches, gray jays) because the stored food is relatively conspicuous (compared to buried seeds), and stored items often can be detected by a forager using visual cues.

Research on the memories of food-storing rodents has been less extensive, but the role of spatial memory in cache recovery is nevertheless well established (Jacobs, 1992; Jacobs and Liman, 1991; Macdonald, 1997; Vander Wall, 1991). Unlike seed-storing birds, however, rodents also have a keen sense of smell, which increases their effectiveness as intra- and interspecific pilferers. Rodents are often the most important pilferers of seeds cached in soil by corvids. However, at least in arid environments, they cannot pilfer caches with impunity. When seeds and the soil in which the seeds are buried are very dry, most rodents are unable to detect the weak olfactory signals that the seeds release (Vander Wall, 1993, 1995a, 1998). Under dry conditions, rodents are likely to rely extensively on spatial memory to recover cached seeds. But during wet periods, olfaction is an effective means of pilfering caches.

Caching and foraging microsites

Some animals cache food in a narrow subset of the available caching sites. This behavior is especially prevalent among chickadees and tits that scatter hoard food items in foliage, branches, and bark of trees. In these birds, most of the winter diet is stored in the autumn on the winter territory of a pair or small flock of birds (Brodin, 1994b; Haftorn, 1956a,b, 1974; Lens et al., 1994; Moreno et al., 1981). Cached items are often partially visible (Haftorn, 1954, 1956a,b, 1974; Inki and Suhonen, 1993; Lens et al., 1994; Petit et al., 1989) so that a keen-eyed forager can find caches made by other birds (Inki and Suhonen, 1993; Suhonen and Inki, 1992). In mixed species flocks, the foraging and hoarding sites of species differ (Moreno et al., 1981; Petit et al., 1989; Pravosudov, 1986; Suhonen and Alatalo, 1991); each species avoids caching in sites where the other species forages (Alatalo and Carlson, 1987; Suhonen and Alatalo, 1991). Within species, the storage sites used in the autumn are similar to the foraging sites used later in the winter (Haftorn, 1956b; Lens et al., 1994; Petit et al., 1989). Members of a population or small monospecific flock can also differ in their use of cache sites (Cowie et al., 1981; Lens et al., 1994; Pravosudov, 1986). For example, Brodin (1994a) found that dominant male willow tits cache in the tops of trees and aggressively exclude subordinate males, which are forced to cache and forage in lower portions of the same trees. Willow tits gather food from portions of the tree where conspecifics forage and cache it in portions of the tree that they defend (Brodin, 1994a). Although differences in foraging and hoarding sites are known to exist in these bird species, it has not been demonstrated that this niche separation significantly lowers pilferage rates.

How much food do scatter hoarders get back?

The model of the evolution of hoarding behavior proposed by Andersson and Krebs (1978) holds that hoarding can be adaptive if the hoarder is more likely than any other animal to

recover its own items. The high levels of pilferage documented seem to challenge that condition, at least for many species that scatter hoard food for long periods. There is relatively little information available on the critical question of how much the hoarder can recover because it is extremely difficult to follow the histories of individual caches in the field. Some studies have reported digging success rate (number of caches found/number of attempts), but this is a completely different statistic than the proportion of cached food recovered (number of own caches found/number of caches made). The caches of an individual are numerous, are widely scattered, and recovered over a period of hours to months. These conditions make it very difficult to monitor caches to determine what proportion is eventually reclaimed by the animal that made them. Despite these difficulties, several studies shed light on this important question.

Stevens and Krebs (1986) used tiny magnetically sensitive electronic switches stationed near real marsh tit caches to measure cache recovery. Each bird that hoarded food wore a small magnet on its leg. Over 2 days, 23.7% of the switches were activated, suggesting that the hoarder had recovered that many caches. Recovery rates declined to zero after about 3 days because pilferers had taken the rest of the seeds. Daly et al. (1992) used traces of dye in the feces of rodents to show that between 10 and 16 animals from four rodent species had pilfered food from the scattered caches of five Merriam's kangaroo rats. However, based on the frequency and intensity of dye in the feces, none of the pilferers made as much use of the caches as did the original hoarder. Ekman et al. (1996) used radio-ptilochronology to determine that Siberian jays in Sweden were seven times more likely to recover food items they had stored than was any other group member. A similar study on willow tits found a 5:1 recovery advantage for the hoarder (Brodin and Ekman, 1994). The degree of pilferage by other bird species and nonflock members was not measured, but because only a small proportion of the labeled food was accounted for, the amount pilfered could have been substantial. Although few in number, these studies all support the conclusion that food-hoarding animals have an advantage over other individuals when they harvest cached food.

Recaching of pilfered food

It is widely recognized that food-hoarding animals recache many of the items that they take from caches (Clarke and Kramer, 1994a; Daly et al., 1992; DeGange et al., 1989; Grubb and Pravosudov, 1994; Haftorn, 1954, 1956a, 1974; Hutchins and Lanner, 1982; Källander, 1993; Macdonald, 1976; Rice-Oxley, 1993; Waite, 1988; Waite and Reeve, 1992). Vander Wall and Joyner (1998), for example, found that 75% of radioactive Jeffrey pine seeds cached by yellow pine chipmunks were found in two cache sites, 29% of the seeds were found in three sites, 9.4% were found in four sites, and 1.3% were found in five sites over a 3-month period. These studies make it clear that cached food is not a static resource that animals simply establish, monitor, and consume as needed, but a dynamic food supply that animals are continually rearranging.

A number of explanations have been offered for the existence of recaching, and four of these are relevant to this discussion. The first three assume that the hoarder is retrieving its own food, and the fourth assumes that the food is found by a pilferer. First, many scatter-hoarding animals, when confronted with a rich ephemeral food supply, rapidly sequester the food in caches near the food source (Bardin and Markovets, 1991; Daly et al., 1992; Jenkins and Peters, 1992; Jenkins et al., 1995; Macdonald, 1976). This behavior results in a high concentration of stored food around the source. To forestall pilferage of these concentrated food caches, the food hoarder often recovers and redistributes the caches within a few hours or days. Recaching, in this context, is a way of reducing pilferage when caches are concentrated (Brodin, 1992, 1993; Waite and Reeve, 1992, 1995) or made in the presence of potential pilferers (Emery and Clayton, 2001). Second, scatter-hoarding animals may retrieve buried food to monitor the condition of their food reserves (see DeGange et al., 1989). Checking cache sites might be valuable if food is perishable or if it might germinate. Third, animals might dig up cached food as a means of updating their memories (Brodin, 1992; DeGange et al., 1989; Grubb and Pravosudov, 1994). Studies of cache-site memory have generally been conducted over short time spans and in small, artificial, structurally simple environments, so there is reason to be skeptical about accurate spatial memory of thousands of sites scattered in an animal's home range for periods of one to several months. Memory of cache sites in black-capped chickadees appears to decline after about 1 month (Hitchcock and Sherry, 1990). On the other hand, precise, long-term spatial memory seems to be well established in species such as nutcrackers (see Balda and Kamil, 1992). And finally, recaching food may occur after pilferage of caches. Pilferers gain recovery advantage by moving food items to new cache sites. By taking the food and recaching it, the new cacher has more information concerning the whereabouts of that food item than any other animal in the community, and therefore, it has a slight advantage in eventually obtaining the food.

A reassessment of caching behavior

The data reviewed thus far reveal three aspects of scatter-hoarding behavior. First, pilferage rates are often so high that an animal's caches can be decimated within days or weeks of preparation. Second, kin selection cannot be invoked to explain the high rates of pilferage observed. The behavior of food-hoarding animals indicates that they are serving their selfish interests. Third, the hoarder has an advantage in recovering stored food items, but this advantage is often small compared with the combined effects of all the intra- and interspecific pilferers. If cached items are not recovered promptly, the advantage may be transient. Despite the ephemeral nature of individual caches, food storing is a central element of the overwintering strategies of many temperate zone birds and mammals. How can food hoarding be maintained under these conditions? We believe there are several explanations, and the appropriate explanation varies with environmental conditions. We propose that food-hoarding animals exhibit one or more of three strategies to cope with cache pilferage: pilferage avoidance, pilferage prevention, and pilferage tolerance.

Pilferage avoidance

Short-term scatter hoarders avoid most of the pilferage that might otherwise occur by retrieving food items quickly. For species such as marsh tits, northwestern crows, and eastern chipmunks, cache residence times range from hours to a few days (Clarke and Kramer, 1994a; Cowie et al., 1981; James and Verbeek, 1983), so food is retrieved and eaten before much pilferage can occur. Some of these animals (e.g., northwestern crows) appear to have evolved short-term hoarding because that is the most effective way to regulate their body mass and internal energy stores (James and Verbeek, 1983; Lucas and Walter, 1991; Pravosudov and Grubb, 1997a,b). Others (e.g., eastern chipmunks) appear to be "forced" to be short-term scatter hoarders by pilferers that decimate their stores if they do not retrieve them quickly. In yet others (e.g., marsh tits), both of these factors act in concert to produce a caching

program that works in an environment with high levels of pilferage.

Pilferage prevention

Species that are compelled to be long-term hoarders by food and environmental contingencies must be able to control pilferage. Larder hoarders do this through aggressive defense of a territory or the larder itself. This option is available only to relatively aggressive species that can protect the larder. Some scatter hoarders that feed in specialized microhabitats also appear to prevent high levels of pilferage through a combination of cache site selection and social dominance (see Moreno et al., 1981). For examples, pairs of European nuthatches experience relatively low rates of pilferage because other nuthatches are excluded and few birds other than nuthatches can extract hidden food items from deep crevices in the bark of trees. Yet other species of scatter hoarders, such as nutcrackers, attempt to prevent pilferage by moving food out of habitats with numerous competitors into areas where the potential for pilferage is much lower (see Hutchins and Lanner, 1982).

Pilferage tolerance

Many species of long-term hoarders that live in environments with high rates of cache loss have evolved mechanisms for tolerating pilferage. In these species, individuals cannot avoid or prevent pilferage (as described in the preceding paragraphs) but instead compensate by pilfering caches of other animals. In other words, pilferage is reciprocal, and as such, it can be tolerated. This notion is consistent with both the high rates of pilferage observed and the propensity of pilferers to recache pilfered food. Species that appear to tolerate pilferage include those that live in social groups and cache in the foliage of trees (e.g., tits, chickadees, and certain jays, *Perisoreus* spp.) and solitary rodents that occupy broadly overlapping home ranges and cache seeds or nuts in the ground (e.g., yellow pine chipmunks; fox, gray, and red squirrels, *Sciurus vulgaris*; field mice, *Apodemus* spp.; heteromyid rodents; and various species of tropical rodents such as agoutis, *Dasyprocta punctata*).

We assert that in these species, the advantage to the hoarder in retrieving food it has hidden is greater than that to other animals, but not always by a wide margin. In nonterritorial or social species, there are often many potential pilferers and only one hoarder for each stored food item. In these situations, the combined ability of the pilferers to find hidden food may be greater than that of the hoarder. Consequently, the hoarder may get back only a small percentage of the food it has hoarded. However, most of the stored food in the environment has been stored by conspecifics, and the hoarder is likely to be an effective pilferer of the caches of these animals (Suhonen and Inki, 1992). The end result is that each animal obtains a portion of the stored food reserve, but the items it eventually eats are not necessarily those that it initially cached.

The greatest challenge to this theory of reciprocal pilfering is that it is vulnerable to exploitation by cheaters: animals that harvest cached food but that do not cache food themselves (Andersson and Krebs, 1978; Källander, 1978). We argue here and demonstrate in the next section that this is not necessarily the case. The most effective pilferers are likely to be conspecifics: animals that eat the same foods and forage in the same places for those foods (see Suhonen and Inki, 1992). Consider a cheater (behavioral mutant) that does not scatter hoard food but exhibits all other species-typical behaviors. This individual would be able to pilfer caches, but the damage it might inflict on a population of food hoarders is limited. First, because this individual does not store food, the amount of food it can pilfer is limited to what it can consume. Further, because most food hoarding occurs during periods of food abundance when unstored food is plentiful and more conspicuous than cached food, a cheater is unlikely to have a significant impact on the stores of its food-hoarding neighbors at this time. The cheater's main impact will probably come when the period of food abundance begins to wane. Unlike the cheater, food hoarders are expected to pilfer far more than they can consume, recaching the excess, which they should do to obtain a recovery advantage. Second, once the period of food scarcity has begun, the cheater's rate of energy acquisition will be lower than that of a food-storing conspecific because it will not share any of the recovery advantages that the hoarder enjoys (i.e., precise spatial memory of cache sites). It is conceivable that under ideal conditions (e.g., mild winters), a nonhoarding cheater could survive and even flourish at the expense of conspecific hoarders. However, all of the species that appear to tolerate pilfering inhabit seasonal and variable environments with a distinct season of food scarcity. During "hard" years, food hoarders will have a distinct advantage over a nonhoarding cheater. The model in the next section evaluates a more complex and realistic cheating strategy.

The reason that cheating usually does not succeed is that costs of scatter hoarding are probably small relative to potential gains. The direct costs of hoarding (energy expended and risk of predation) are probably similar to those of foraging. Indirect costs include the effect of uncompensated pilferage. If the advantages of hoarding (increased knowledge and certainty of a food supply) outweigh the costs, a food-hoarding individual will outcompete a nonhoarding cheater. We assert that in a harsh and variable environment, the benefits of caching will greatly outweigh the costs over the long term. The many species of scatter-hoarding birds and mammals that appear to tolerate pilferage are simply those that could not be invaded by cheaters in the past because no cheater strategy was as profitable as a scatter-hoarding strategy.

Pilfering should act as an important selective force on the behavior of scatter-hoarding animals (Clarke and Kramer, 1994a), but we believe that past studies have not focused on the critical aspect of this issue. What is important is not how much pilfering occurs, but what the pilferer does with the food that it discovers. If the pilferer recaches the food, and if pilfering is reciprocal, then long-term scatter hoarding can persist unless some alternative form of food storage (larder hoarding or internal energy storage) provides more benefits.

A model of reciprocal pilfering

The cheating strategy that seems most likely to be damaging to a population of scatter hoarders is pilferage of scattered caches and storage of pilfered items in a defensible larder. We used a genetic algorithm to model the evolution of food-hoarding behavior and investigate the conditions under which this cheating strategy would be successful. Genetic algorithms are widely used in computer science and other fields to solve complex optimization problems (Forrest, 1993; Holland, 1992; Mitchell, 1996). They do so by imitating the process of evolution: various possible problem-solving "strategies" are generated by random mutation and recombination, these strategies compete with each other in solving a problem, success of the strategies is indexed by an appropriate measure of fitness, and a new generation of strategies is created by random mating of the strategies with the highest fitnesses in the previous generation. This modeling approach has only recently been applied in biology, but is useful as an alternative to stochastic dynamic programming when the possible states of a system are too numerous or complex for stochastic dynamic programming to be

feasible (Clark and Mangel, 2000; Price et al., 2002). In biologic applications of genetic algorithms such as this model of food-hoarding behavior, the model does not necessarily represent a realistic mechanistic description of the system. Instead, we use it as a computational tool to help understand how reciprocal pilferage might influence the maintenance of scatter hoarding in a population.

The model is described in detail in the appendix, but its key features are summarized here. We developed the model for small solitary rodents with overlapping home ranges, but it could be modified to represent other situations. Animals search for food items that can be stored or consumed during a hoarding season when no breeding takes place. New food items are produced in excess of the requirements of the population initially, but at a decreasing rate during the first half of the hoarding season and not at all during the second half; i.e., animals have to rely on stored food to survive through the hoarding season. We assumed that fitness at the end of the hoarding season is directly proportional to the number of items remaining in an individual's stores at that time. This assumption was based on the idea that an animal can use the food in scattered caches and larders during the following breeding season to improve its body condition, thus increasing its reproductive success.

While foraging, animals can harvest newly produced (public) items or pilfer items from scattered caches or larders made by other individuals. Scatter hoards of other individuals are characterized by apparency values, representing their reduced detectability compared with that of public food. Because scatter-hoarded items, particularly those made by rodents, are typically buried a few centimeters below the soil surface (Vander Wall, 1993), the food items are not visible and the odor cues that they emit should not travel as far as the cues of food items on the surface that have not yet been harvested and cached. Therefore, we specified the apparency of scatter hoards as $appscat < 1$. If not eaten, the pilfered items can be either scatter hoarded or larder hoarded and thus become available for pilferage by other members of the population in subsequent foraging bouts.

We also used an apparency parameter for larder hoards of other individuals (*applard*), which represented the relative probability of detecting a burrow of another individual while searching for food. No data are available for estimating *applard*, so we used values between 1 and 3 in the model. A value of 1 implies that the probability of detecting a burrow while foraging is the same as the probability of encountering a food item on the surface of the ground; a value of 3 implies that the former probability is 3 times the latter. We believe that use of values for *applard* in this range is conservative with respect to assessing the likelihood that scatter hoarding could evolve and be maintained in the face of high rates of cache pilferage. Although entrances to rodent burrows can be somewhat cryptic, they are more conspicuous than are individual seeds. Therefore, burrow entrances should be more noticeable than are seeds to a foraging rodent. Furthermore, rodents likely are able to learn the locations of burrows they encounter, because these are potential hiding places in case of danger.

Different apparencies of scatter hoards and larder hoards represent one element in the trade-off between these two strategies. Although larder hoards are more apparent, and thus more likely to be detected and pilfered, they can be defended by the owner of a burrow, whereas scatter hoards are indefensible. However, we assumed that an animal that finds an undefended burrow and begins pilfering food from it continues to do so until the end of 1 day of foraging or until the owner returns to defend the larder hoard (Daly et al., 1992; Elliott, 1978). This represented the risk of catastrophic loss of larders compared to gradual attrition of scattered caches, which are found at a lower rate by potential thieves.

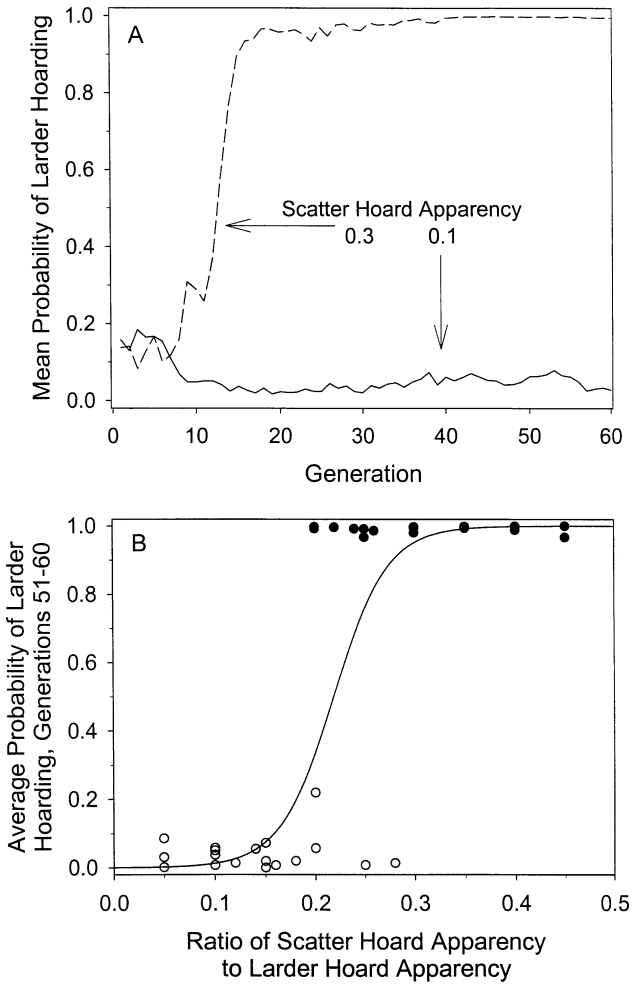


Figure 2
(A) Illustration of evolutionary change in the average probability of larder hoarding in populations simulated by using a genetic algorithm. In both examples, apparency of larders was 1.0, and average probabilities of larder hoarding of individuals were approximately 0.15 initially. (B) Establishment of larder hoarding in simulated populations as a function of the ratio of scatter-hoard apparency to larder-hoard apparency. All simulations started with average probabilities of larder hoarding of approximately 0.15. Filled circles represent cases in which larder hoarding became established by the last 10 generations; open circles represent cases in which larder hoarding did not become established. The line represents probability of larder hoarding becoming established as a function of the ratio of apparencies as estimated by binary logistic regression (logit $= -8.00 + 36.59 \times$ ratio; McFadden's $\rho^2 = 0.61$).

Each individual was characterized by two traits: its probability of larder-hoarding food items and its propensity to defend its larder hoard as a function of the amount stored in the larder. Because we were interested in the likelihood that scatter hoarding could persist in the face of cheaters that pilfered scattered caches and moved them into larders, we began simulations with populations of individuals with low probabilities of larder hoarding and moderate propensities to defend their larders. We assumed a moderate amount of genetic variation underlying these traits in initial populations (see the Appendix for details), and considered the evolution of these traits over 60 generations for various combinations of scatter hoard and larder hoard apparency.

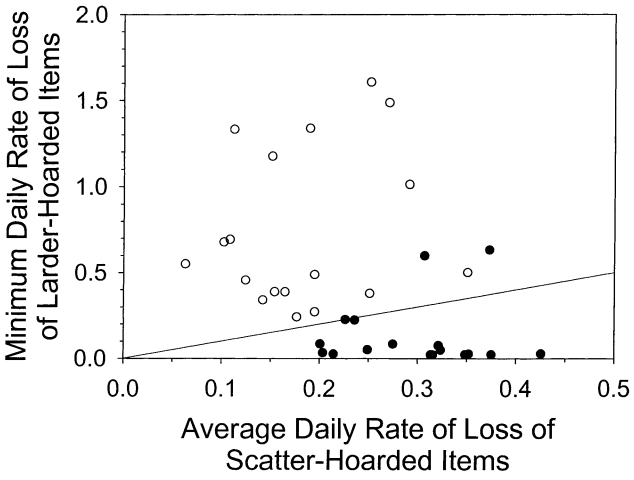


Figure 3
Average daily rate of loss of scatter-hoarded items and minimum daily rate of loss of larder-hoarded items in the first 10 generations of simulated populations in relation to establishment of larder hoarding in these populations. Above the line, minimum rate of loss of larder-hoarded items is greater than average rate of loss of scatter-hoarded items; below the line, average rate of loss of scatter hoards is greater than minimum rate of loss of larder hoards. Symbols same as in Figure 2B.

In 35 runs of the model, average probability of larder hoarding always remained less than 0.2 or increased rapidly to more than 0.95, usually within 10 generations (Figure 2A). Therefore, we used logistic regression to analyze the relationship between the probability that larder hoarding would spread in a population and the apparency of scatter hoards and larder hoards. This probability was closely related to the ratio of scatter-hoard apparency to larder-hoard apparency (Figure 2B). For ratios less than 0.2, high probabilities of larder hoarding never evolved; for ratios greater than 0.3, high probabilities of larder hoarding almost invariably evolved.

Most change in average probability of larder hoarding in populations occurred in the first 10 generations of our simulations, so we examined the rate of loss of scatter hoards and larder hoards within this time to help elucidate the mechanisms underlying evolution of larder hoarding in our model. Because of the greater apparency of larders, items stored in larders were lost at a much greater rate (mean = 186% per day) than were scattered caches (24%/day). In addition, the coefficient of variation in rate of loss of larder-hoarded items (57%) was almost twice that of scattered caches (33%). This was a consequence of the fact that an individual's larder was vulnerable to catastrophic loss if the larder was discovered by another animal while it was undefended. Although the average daily rate of loss of larder-hoarded items exceeded that of scatter-hoarded items in all 35 simulations, the eventual outcome of simulations could be predicted based on the relationship between the *minimum* rate of loss of larder-hoarded items and the *average* rate of loss of scatter hoards. If one or more individuals in the first 10 generations lost items from larders at a lower rate than the average rate of loss of scattered caches in the population, then larder hoarding usually became established at high levels in these simulations (Figure 3). This occurred because individuals with relatively low rates of loss of larder-hoarded items were able to build up large defensible stores in their larders and, therefore, had very high reproductive success. Moreover, low minimum rates of loss of larder-hoarded items compared with the average rates of loss for scatter hoards occurred at high ratios of scatter-hoard apparency to larder-hoard apparency.

If larder hoarding can become established in a population of scatter hoarders through high rates of cache pilferage, why are there so many scatter-hoarding species? In our simulations, the average daily rate of loss of scatter hoards was 18% in cases in which larder hoarding did *not* become established. This is greater than the median empirical rate of loss for long-term scatter hoarders of 9% (Table 1). Therefore, our model mimics the empirical observation that animals can apparently tolerate high rates of loss of scatter hoards through use of reciprocal pilferage. More importantly, the model shows that a population of scatter hoarders can resist invasion by cheaters that larder hoard even when pilferage rates are quite high. In addition to these basic results, the model suggests that the prevalence of scatter hoarding in communities should depend on environmental conditions that affect the apparency of scattered caches and larders. For example, various rodents have difficulty detecting dry seeds buried in dry soil (Vander Wall, 1993, 1995a, 1998), implying that apparency of scattered caches may be less in dry environments than in wet environments. We will explore these implications of the model elsewhere.

Implications of reciprocal pilfering

Within a population of scatter hoarders (e.g., willow tits, gray jays, Merriam's kangaroo rat, or yellow pine chipmunks), the ability of individuals to pilfer food from one another probably varies. Some pilferers are much better than average, gaining more cached food than they lose, whereas others are poor pilferers, losing more cached food than they gain. This variability may be related to age, social dominance, or foraging methods. Most of this pilferage is associated with recaching, so it may have little impact on the total amount of stored food in the environment. However, because the hoarder has a recovery advantage in finding food it has hidden, this unbalanced pilfering represents a shift in knowledge of the stored food base within the environment from poor pilferers to good pilferers. In a sense, more successful pilferers could gradually increase their "control" of the stored food reserve in an environment. If this advantage influences fitness, then it is likely to have important evolutionary consequences for the population. First, there should be strong selection for aggressive pilfering within a population. This may help to explain why pilfering is so widespread in some species. Second, it could result in more diverse hoarding behavior within a population, as poor pilferers evolve ways of making cached food more secure. This selective force may help to explain the evolution of differential use of hoarding sites among members of tit and chickadee flocks (Baker et al., 1990; Brodin, 1994b; Ekman, 1979), as well as in variable levels of scatter and larder hoarding in heteromyid rodents (Jenkins and Breck, 1998; Price et al., 2000).

Although the most important pilferers are likely to be conspecifics (Suhonen and Inki, 1992), many caches are lost to other species as well. These interspecific pilferers fall into two groups: those engaged in reciprocal pilfering with the hoarder (reciprocating pilferers) and those not so engaged (non-reciprocating pilferers). There are many situations in which interspecific cache pilfering could be reciprocal or nearly so. For example, yellow pine chipmunks and deer mice pilfer each other's cached seeds under wet conditions (Vander Wall, 2000). The cache microhabitats and cache depth profiles of these species overlap broadly, so they frequently encounter each other's caches. Different tit species in mixed species flocks in coniferous forests (e.g., willow tits and crested tits, *Parus cristatus*) appear to encounter food cached by each other (Suhonen and Alatalo, 1991). This

aspect of caching behavior is poorly understood and is in need of study because it may play an important role in species coexistence within communities. If cache pilferage between species is unbalanced, then it may shift the competitive advantage toward those species that are better pilferers even if those species are inferior competitors at feeding sites (Leaver and Daly, 2001). Past studies of species coexistence have focused on foraging efficiency and microhabitat use, but unbalanced interspecific pilferage of caches may also play an important role in this process.

Nonreciprocating interspecific pilfering includes any situation in which an individual pilfers food and either eats the food or disposes of it in a manner such that the original cacher has no possibility of recovering it or finding similarly handled food items. This form of pilferage is very common. For example, when caches are pilfered by nonhoarding animals (e.g., great tits, *Parus major*, stealing marsh tit caches), the original hoarder cannot reciprocate. Likewise, whenever a species that predominantly larder hoards (e.g., San Diego pocket mouse, *Chaetodipus fallax*) pilfers the caches of a species that scatter hoards (e.g., Merriam's kangaroo rat), this loss would not be compensatible (Leaver and Daly, 2001). The pilfering by rodents of caches made by corvids would also fall in this category, because jays and nutcrackers, with their poor sense of smell for most cached foods (e.g., seeds and nuts), are less successful at finding food hidden by rodents. Nonreciprocated pilferage, which is often caused by heterospecifics, appears to be the most damaging form of pilferage. If so, interspecific pilferage (which has received little study) may have been more important than intraspecific pilferage (see Clarkson et al., 1986; Stapanian and Smith, 1978) in shaping the hoarding behavior of animals.

A number of authors have suggested that scatter-hoarded food can be regarded as "communal property," which all members of a local population share (Bardin and Markovets, 1991; Covich, 1987; Haftorn, 1954, 1956a,b, 1974; Kawamichi, 1980; Thompson and Thompson, 1980). We disagree. This concept of scatter hoarding assumes that individuals behave altruistically, caching food for the benefit of unrelated conspecifics. It is difficult to understand how such a system could evolve. Further, this notion is not compatible with the caching behavior of many species, which are vigilant during caching and often refrain from caching when competitors are nearby (Burnell and Tomback, 1985; Heinrich and Pepper, 1998; Källander, 1978; Lahti and Rytkonen, 1996; Stone and Baker, 1989). It is also incompatible with the demonstrated selfish use of cached food (Brodin and Ekman, 1994; Ekman et al., 1996; Härdling et al., 1995). Instead, we believe pilferage tolerance is a form of reciprocity. Unlike reciprocal altruism (Trivers, 1971), reciprocal pilfering is not based on the exchange of helpful acts but is, instead, reciprocal exploitation. A similar theory has been proposed to explain the evolution of food sharing in humans (Blurton Jones, 1987). For this form of reciprocity to be evolutionarily feasible, several conditions must be met, some similar to reciprocal altruism and some different. First, as in reciprocal altruism, the pilferage must occur among nonrelatives to distinguish the interaction from kin selection (but see Rothstein, 1980). Second, there is an unequal cost/benefit ratio to the exploitative act; i.e., there must be a large disparity between the net benefits of the hoarder and cheater behavioral strategies. Pilferage is potentially harmful to the hoarder, but its effect is made much smaller by opportunities to pilfer similar foods. In contrast, there are large net benefits of food storage to those that cache food relative to the small and limited benefits to individuals that attempt to exploit the caches of others without caching themselves. And third, reciprocal altruism often occurs over a long period of time. But because most scatter hoarders have thousands of caches spread across their home range, reciprocal pilfering can occur nearly simultaneously, with the interactants separated in space. Reciprocal pilfering can result in a situation that appears to be collective use of caches by a group or population, but the behavior does not require an altruistic mechanism and can be driven by the selfish interests of individuals.

APPENDIX

General description of the model

We imagined a population of 20 individuals harvesting and storing food during a nonbreeding season of 100 days. Storable food was produced at a linearly decreasing rate during the first 50 days; once all of this public supply was harvested, individuals had to rely on their stores to survive the nonbreeding season. Each individual was allowed 20 bouts of foraging per day and had to harvest one item, either from the public supply or from its own stores, to survive the day.

In each foraging bout, individuals had the following options: consume one food item from its own stores, forage for consumption, forage and scatter hoard or larder hoard if successful at finding a food item, or remain in the burrow defending a larder. The first two options took priority; i.e., until an individual fed once each day, it did not store additional food. While foraging, individuals encountered public items, as well as scatter hoards and burrow entrances of other individuals, with probabilities determined by the apparency values for scatter hoards and larder hoards described in the text. Therefore, a successful foraging bout might involve pilfering an item that had previously been scatter hoarded or larder hoarded by another animal. Once an individual had met its daily requirement, which often happened in the first bout early in the hoarding season, then either it stored new items found while foraging on subsequent bouts during the same day or it remained in its burrow. When it found new items, its genotype determined whether they were scatter hoarded or larder hoarded.

Some individuals died during the hoarding season, either because they were taken by a predator with low probability or because they were not able to acquire a meal each day. The latter happened occasionally by failure to find food early in the hoarding season, when new food was being produced each day. Starvation also occurred in the second half of the hoarding season if the food stores of an individual were depleted. At the end of each generation, the survivors mated to produce 20 individuals to start the next generation (i.e., generations were non-overlapping). Reproduction was a stochastic process with fitness of each survivor proportional to the amount of stored food remaining for that individual at the end of the hoarding season.

Each individual was characterized by two traits: its probability of larder hoarding and its propensity to defend its burrow as a function of how much food was stored in the burrow. The first trait simply determined the likelihood that an individual would larder hoard a newly acquired item, regardless of whether that item was harvested from the public supply or stolen from another animal's scatter hoards or larder hoards. We defined probability of burrow defense as an increasing logistic function of how full the burrow was. Probability of burrow defense was 0.5 when the amount of food stored in the burrow was half of the target amount of food larder hoarded, where the target value was between the minimum amount needed to survive the rest of the hoarding season without further foraging and the maximum amount available if the animal foraged successfully in all its remaining

foraging bouts. An individual's propensity for burrow defense was a value between 0 and 1, which determined the location of its target value within this range; i.e., 0 implied that the target was the minimum amount needed to survive, and 1 implied that the target was the maximum amount available.

Implementation of the model

At the beginning of a run of the model, we specified apparencies of scatter hoards and larder hoards, probabilities of predation in the open and in a burrow, heritability for probability of larder hoarding and propensity for burrow defense, average probability of larder hoarding, average propensity for burrow defense in the starting population of 20 individuals, and segregation variances for these last two parameters. We varied apparencies of scatter hoards from 0.05–0.90 and apparencies of larder hoards from 1–3 in various runs. Values of other parameters were fixed in the runs reported in this article, although we explored the sensitivity of model output to variation in these parameters. Results of a full sensitivity analysis will be reported elsewhere. Probabilities of predation were set at 0.0001 in the open and in the burrow during each foraging bout. Heritability was fixed at 0.80 for both probability of larder hoarding and propensity to defend the burrow, probability of larder hoarding in the initial population followed a logistic distribution with a mean of about 0.15, and the propensity for burrow defense in the initial population followed a logistic distribution with a mean of about 0.50.

We set the number of food items produced during each season at 5% more than the number needed for all individuals to survive for 100 days if all harvested the same number of items and no items were left over at the end of the season. We assumed that individuals had alternative nonstorable food items (e.g., insects) available for days 1–5 but relied on storable items (e.g., seeds) for immediate consumption as well as storage from days 6–100. Storable items were produced according to a linearly decreasing function on days 1–50, such that the total number of items produced was 1.05×20 individuals $\times$ 100 days $= 2100$; i.e., 82 items on day 1, 81 on day 2, 79 on day 3, . . ., 2 on day 50 (these numbers were based on a linear function but rounded off to integers). We modeled foraging as a stochastic process with a baseline probability of complete failure of 0.01 on the first day when 82 items were produced and no scatter hoards and larder hoards were available for pilferage. This enabled us to compute the rate of encountering food items, λ, for each individual during each bout as a function of food availability, including public food, scatter hoards, and larder hoards, with the amounts in the latter two categories adjusted by their apparencies. Specifically,

$$\lambda = \text{forage}_i \times \left(\frac{-\ln(0.01)}{20 \times 82^{1.5}}\right) \times (\text{food available})^{1.5}$$

where forage_i indicates the foraging efficiency of individual i, drawn from a normal distribution with mean = 1 and SD = 0.1. For an individual with a foraging efficiency of 1 at the beginning of the first day when the number of food items available was 82, $\lambda = 0.23$, which produced a detection probability of $1 - \exp(-\lambda) = 0.21$ per bout, which translated to a probability of finding one or more items on the first day of 0.99, i.e., probability of complete failure on the first day of 0.01.

The model began each generation by initializing a set of arrays for the state of each individual (satiated = 0, hungry = −1, or dead = 999), the number of items scatter hoarded and larder hoarded by each individual, the probability of burrow defense for each individual, and the foraging efficiency of each individual. An array was also used to keep track of the number of pubic food items available on each day. The program looped through 100 days for each of 60 generations and 20 foraging bouts for each day. For each new day, the public supply was computed as the sum of carryover from the previous day (for all days) plus new production (for days 1–50). For days 6–100, the state of each living individual was set at −1 (hungry).

For the first foraging bout on each day, individuals with any items stored in larder hoards or scatter hoards were assumed to use one of these items to satisfy their daily food requirements, and their states were set at 0 (satiated). If individuals had only larder hoards or both larder hoards and scatter hoards, they used a larder-hoarded item and were assigned a probability of burrow defense of 1; if individuals had only scatter hoards, they used one of these and were assigned a probability of burrow defense of 0. Otherwise, individuals were identified with a flag that specified that the first item they harvested during the day would be used to satisfy their daily food requirement. For all bouts after the first daily bout, probabilities of burrow defense for individuals with state = 0 were determined by the ratio of food stored in the burrow to the target value for size of the larder hoard as described above. The program also determined whether each of these individuals would larder hoard or scatter hoard an item it harvested during each bout by comparing a pseudo-random number from a uniform distribution on the interval [0,1] to the individual's probability of larder hoarding.

For each bout, the program called a subroutine that determined whether each individual was preyed upon. Then individuals that were not defending their burrows were selected for foraging in random order. For individuals that had harvested an item from another animal's larder hoard during the previous bout, the program used a subroutine to determine if the individual was successful at the same burrow during the current bout, based on whether larder-hoarded items remained in the burrow and whether the owner was defending it. Finally, the program used a subroutine to simulate the searching process. The total number of food items available to individual, i, was the sum of public food plus all scatter hoards of other individuals weighted by apparency of scatter hoards plus all larder hoards of other individuals weighted by apparency of larder hoards. This determined detection probability as described above. If a pseudo-random number from a uniform distribution on [0,1] was less than this probability, the individual was successful and the particular item harvested was determined at random based on the proportion of all items available that belonged to a specific category: public items, scatter hoards of individual j for all $j \neq i$, and larder hoards of individual j for all $j \neq i$, with the latter categories weighted by apparencies. Harvested items were either eaten, scatter hoarded, or larder hoarded based on an individual's state and its probability of larder hoarding versus scatter hoarding.

To start the next generation, the program randomly picked a mother and father from among surviving individuals for each of 20 offspring. The probabilities of being picked were proportional to the amount of leftover stores (both scatter hoards and larder hoards) of each individual; i.e., an individual with a large amount of leftover food compared with other members of the population might be a parent of several offspring. We used a standard model of quantitative inheritance to determine offspring phenotypes in generation $t+1$ based on parental phenotypes in generation t:

$$X_0 = N[h^2 X_p + (1 - h^2)\bar{X},\ V_{seg}]$$

where X represented either probability of larder hoarding or propensity of burrow defense, X_0 was the offspring value of

the trait, X_p was the midparent value, $\bar{X}$ was the mean value in the parental population, h^2 was heritability, V_{seg} was the segregation variance, and N[mean, variance] represented a normal distribution (Roughgarden, 1979: 134–140; note that the version of this equation in Clark and Mangel [2000, equation 10.35] is incorrect). We applied the logit transformation to these values to restrict them to the range between 0 and 1.

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