

Review

The history of scatter hoarding studies

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In this review, I will present an overview of the development of the field of scatter hoarding studies. Scatter hoarding is a conspicuous behaviour and it has been observed by humans for a long time. Apart from an exceptional experimental study already published in 1720, it started with observational field studies of scatter hoarding birds in the 1940s. Driven by a general interest in birds, several ornithologists made large-scale studies of hoarding behaviour in species such as nutcrackers and boreal titmice. Scatter hoarding birds seem to remember caching locations accurately, and it was shown in the 1960s that successful retrieval is dependent on a specific part of the brain, the hippocampus. The study of scatter hoarding, spatial memory and the hippocampus has since then developed into a study system for evolutionary studies of spatial memory. In 1978, a game theoretical paper started the era of modern studies by establishing that a recovery advantage is necessary for individual hoarders for the evolution of a hoarding strategy. The same year, a combined theoretical and empirical study on scatter hoarding squirrels investigated how caches should be spaced out in order to minimize cache loss, a phenomenon sometimes called optimal cache density theory. Since then, the scatter hoarding paradigm has branched into a number of different fields: (i) theoretical and empirical studies of the evolution of hoarding, (ii) field studies with modern sampling methods, (iii) studies of the precise nature of the caching memory, (iv) a variety of studies of caching memory and its relationship to the hippocampus. Scatter hoarding has also been the subject of studies of (v) coevolution between scatter hoarding animals and the plants that are dispersed by these.

Keywords: scatter hoarding; cache retrieval; spatial memory; optimal cache density; hippocampus

1. INTRODUCTION

Many species of birds and mammals are well-known food hoarders. Some invertebrates also store food, the most famous example being honey production in bees. After collecting nectar, the bees will transform it into more durable honey and store it in the hive. Such a strategy, when all food is stored in a central site, is called larder hoarding and it is usually employed only by animals that are able to defend such a resource against scroungers. The theme of this issue of *Philosophical Transactions of the Royal Society* is scatter hoarding, a strategy when animals disperse caches in many different locations, in many cases with one single food item in each one. Scatter-hoarded food can usually not be guarded and defended. Instead, it is protected by concealment in combination with a low cache density. If a scrounger finds a larder, the hoarder may lose its entire supply of winter food. If the scrounger finds a scatter-hoarded nut, the loss is usually negligible. In many scatter hoarding species, one individual may disperse thousands of caches over a large area. Most hoarding animals can be categorized as either scatter or larder hoarders, but there are exceptions to this. Eastern chipmunks *Tamias striatus*

provide an interesting example that illustrates the difference between larder and scatter hoarding (Clarke & Kramer 1994). Older dominant individuals that are able to defend their caches against scrounging conspecifics are larder hoarders, whereas younger subordinate individuals are scatter hoarders.

Most scientific research on scatter hoarding has been on birds, but there are also many studies on mammals. This will be reflected in this article: the emphasis will be on birds, but with examples also from mammals. Invertebrates do not scatter hoard and will thus not be treated further here. By 'history' in the title, I mean that I intend to present a review over the development of the field. I will start by the oldest studies but also include recent studies that I think are important. A discussion of studies before 1990 that I have not included can be found in Vander Wall's (1990) book 'Food hoarding in animals'.

Scatter hoarding is in many cases a conspicuous behaviour. Many of us have observed a titmouse, jay or a squirrel grab a nut from a bird feeder and rapidly transport it away from the source before it is cached somewhere in the surroundings. After caching, it will return to the feeder and grab another nut. The frequency of visits will be high and it will be able to secure many more nuts from the feeder than non-hoarding competitors.

There are very many studies on cache retrieval, spatial memory and the hippocampus in scatter

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One contribution of 10 to a Theme Issue 'Integrating ecology, psychology and neurobiology within a food-hoarding paradigm'.

hoarding animals; hence, I will discuss these topics at some length. Other topics that have been studied in scatter hoarders include the evolution of scatter hoarding behaviour as a strategy, studies of how animals should disperse caches to minimize cache loss, and the coevolution between scatter hoarders and plants that they may disperse.

This Theme Issue was initiated at a scatter hoarding meeting at Cornell University in August 2008 that was held to commemorate the 30 year anniversary of an influential theoretical paper by Andersson & Krebs (1978). Hence, I will refer to studies published before that as 'early' and studies published after that as 'modern'.

2. THE FIRST RECORDS

Observations of scatter hoarding birds must have been done by people interested in nature for a long time. A study that resembles a modern well-designed experiment in many respects was published already by von Pernau in 1720. In 'Angenehme Landlust' (agreeable country pleasures), baron Johan Adam Friedrich von Pernau provide detailed accounts for how various species of birds should be captured and kept alive in captivity. In the chapter on 'Meise' (the family Paridae that consists of titmice and chickadees), he describes how marsh tits *Poecile palustris* (a European close relative to the chickadees in America) store hemp nuts in captivity. In a few extracted sentences, freely translated from German black-letter writing, the baron tells us: 'The one who searches for some kind of mind (German 'Verstand') in animals should bring a marsh tit into a room... put a tree in the room... after starving the bird for half a day provide it with hemp nuts... it will carry away three to four nuts... cache some of these... keep on doing this until there are no more nuts... during retrieval the birds seem to consider caching locations in such a way that its behaviour can not be explained by instinct'. Clearly, von Pernau (1720) understood that the tits were using memory to relocate cached nuts.

The great Swedish naturalist Linnaeus appears not to have been that modern in his views on the functionality of scatter hoarding. In his lectures, in Uppsala, he told the students the following about the Eurasian nutcracker *Nucifraga caryocatactes*: 'Very rare, stays in hazel forests, and eats as many nuts as she can, then she caches, and, while she uses clouds as landmarks, say the farmers, she will not relocate anything of her treasure, since the landmarks will disappear' (Lönnerberg 1913). To be fair to Linnaeus, this may not be his own view on food hoarding as he quoted a popular belief among farmers. The very fact that he pointed out that this was a quotation from farmers suggests that he may have doubted whether this was correct. The nutcracker and its close American relative Clark's nutcracker, *Nucifraga columbiana*, may be the most highly specialized food hoarders in the animal world. In autumn, these two species spend most of the daylight hours scatter hoarding pine or hazel nuts. What Linnaeus' story tells us is that nutcracker hoarding behaviour must have been known among farmers in Sweden around 1700.

3. EARLY ORNITHOLOGICAL FIELD STUDIES

Until the early 1900s, most ornithological observations were done with a rifle. When binoculars became widely available, observations of animal behaviour, especially in birds, started. Two ornithologists made pioneering field studies of scatter hoarding in the 1940s and 1950s: Svein Haftorn in Norway and P. O. Swanberg in Sweden. Haftorn (1956b) studied hoarding in three species of tits that occur in the boreal coniferous forest, the willow tit *Poecile montanus*, the coal tit *Periparus ater* and the crested tit *Lophophanes cristatus*. Swanberg (1951) studied hoarding in the Eurasian nutcracker.

Both these investigators collected impressive amounts of data as they spent considerable time in the field over several years. However, data are not as reliable as in more recent studies of this type as sampling methods were not standardized (§8), the birds were simply *observed*. Still, the hoarding rates calculated by Haftorn (1956b) are remarkably similar to those calculated later with standardized methods: about one item stored per minute and individual when hoarding rates peak in September (e.g. Brodin 2005a). This means that individual birds would store between 50 000 and 60 000 food items in one autumn. This is not an exaggeration; in the cold region at the White Sea in Russia, the total amount hoarded in an autumn has later been estimated to be around three times as much during spruce mast years (Pravosudov 1985).

Haftorn (1956a) shot some willow tits in the winter in order to investigate their stomach contents. Willow tits prefer a specific type of seeds, hemp nettle nuts *Galeopsis* spp., which is not stored by other titmice that occur in the coniferous forest. These nuts are available to the birds only in September and October before the plants wilt and the ground becomes covered by snow. Even in February, the most notable component in the tits' stomachs was hemp nettle nuts that must have been stored at least four months earlier. This showed that willow tits store seeds in autumn when they are abundant and consume them in winter when food is scarce. Haftorn's (1956a) observations have later been verified by year-round faeces analyses in a population of Swedish birds (Jansson 1982).

Parids may store food for even longer intervals than suggested by Haftorn's stomach analysis. In a letter, Swanberg told me about an isolated cottage in the forest in his fieldwork area on Mount Billingen, southwestern Sweden. The people who used to live there had been keen on feeding birds, but during the last year after feeding had stopped, Swanberg would regularly see marsh tits appear with non-native hemp nuts that could only have been available from bird feeders the preceding winter. Marsh tits are resident in lifelong territories and there were no other bird feeders in the vicinity. These nuts must have been cached at least for a year.

Even though Swanberg (1951) did not observe colour-banded birds, he took advantage of the fact that the Eurasian nutcracker is highly territorial in its breeding territory. This means that only the local breeders that own the territory will store in it. In one

particular territory, Swanberg (1951) followed the hoarding pair from a lookout position. He could fairly accurately separate the hoarding individuals from each other without actually identifying the male and the female as he knew the distance to the hazel coppices from which the nutcrackers harvested their nuts and the approximate time it takes a nutcracker to fill its pouch. When hazel nuts are available, nutcrackers are industrious. As soon as a nutcracker has filled its pouch, it will return to the territory and make a new cache in which it stores 15–20 nuts. In less detail, he could also monitor the hoarding activities of several adjacent pairs, and by comparing his observations over days he could calculate the change in hoarding rate throughout the autumn. In this way, he could estimate that the individuals in this pair made around 8000 caches per individuals in one autumn.

The most important discovery he made must be the high recovery success. In winter, caches are covered by snow, and the nutcrackers make excavation holes to get access to them. As nutcrackers have the habit of leaving cracked shells at the excavation holes, he could in most cases determine if a particular excavation had been successful or not. As some excavated nuts may have been removed from the holes or stolen by rodents, his estimate is conservative. The success was rather constant throughout the whole winter, almost 90 per cent of the excavation holes contained cracked nutshells. This means that the nutcrackers must have been almost 100 per cent accurate in their ability to relocate caches. The snow cover means that possible cache cues such as disturbed soil or smell of food were not available. Swanberg (1951) was positively sure that the nutcrackers used memory to relocate caches.

Similar field studies have been made somewhat later on coal tits and willow tits in Britain (Gibb 1960), European nuthatches *Sitta europaea* (Löhr 1956) and marsh tits in Germany (Löhr 1950) and black-capped chickadees *Poecile atricapillus* in America (Odum 1942), but these studies describe the general biology of these species and are not as focussed on food-hoarding behaviour as Swanberg's (1951) and Haftorn's (1956a) studies were.

4. WHY SCATTER HOARDING?

A term such as scatter hoarding may seem obvious today, but it appears not to have been used until Morris (1962) published a study on hoarding behaviour in captive green acouchis *Myoprocta pratti*, a South American forest-dwelling rodent. In contrast to many other mammals, this species buries food items singly. Morris (1962) kept a pair of acouchis in a large cage, approximately 2 × 3 m. The cage had a metal floor that made hoarding impossible. After some time, he spaced out 16 metal trays evenly in the cage. One of the trays was filled with small dog biscuits (a preferred hoarding item for acouchis) and the other 15 with sand (a preferred hoarding substrate). Morris (1962) could show that the acouchis distributed caches evenly between trays, and that the reason for this preference was a desire to disperse caches

rather than some other preference (e.g. for specific trays, for optimizing transporting distances, etc.).

The great Dutch ethologist Tinbergen (1965) examined how a fox *Vulpes vulpes* scatter hoarded gull eggs. A seaside colony of black-headed gulls *Larus ridibundus* was only accessible to the fox if it crossed sand dunes that surrounded the colony. By checking these dunes regularly for tracks, Tinbergen (1965) could monitor the fox's visits to the gull colony over a whole summer. By following the fox's tracks, he could also find buried food such as gull eggs, dead gulls and rabbits. In order to examine the significance of scatter hoarding, he positioned 100 chicken eggs 10 m apart in a line across the dunes. He buried the eggs, just as the foxes, below 3 cm of sand. To control that his experimental manipulation or smell did not attract foxes, he also made 100 fake caches, with no egg buried. As fake caches were never examined by the foxes, he could show that the fox located cached eggs by their smell, not needing to remember exact caching positions. Scattering proved to be very important to protect caches from hedgehogs *Erinaceus europaeus* that were also able to locate buried eggs by smell, although not as successfully as foxes.

In another experiment, which did not specifically concern scatter hoarding, Tinbergen *et al.* (1967) specifically demonstrated the protective effect provided by spacing out food resources such as caches. At the same gull colony as in the fox tracking experiment, carrion crows *Corvus corone* would regularly search for gull eggs. The experimenters painted chicken eggs so that they resembled gull eggs and laid out the eggs on the ground, but in positions where they were reasonably well camouflaged, for example, in grass tufts and moss. By varying the concentration of eggs within experimental plots, they could show that inter-egg distance was an important factor for egg survival. The higher the density of eggs was, the faster the crows would find them.

5. SCATTER HOARDING AND MEMORY: A PIONEERING STUDY

Studies of morphological correlates of caching memory have been focussed on a particular part of the brain, the hippocampus, henceforward Hp which I will use for 'hippocampus', 'hippocampi' and 'hippocampal'. This word means sea horse, and from some angles the human Hp may look like a seahorse. The reason for such a focus on the Hp is that it has been shown to be important for spatial memory. It all started in 1953 when Henry Gustav Molaison, known as H.M., a patient who suffered from severe temporal lobe epilepsy, had his medial temporal lobes (and thereby most of the Hp) removed to relieve his seizures. Surprisingly, much of his ability to form new memories disappeared while he still accurately remembered pre-operation facts (Scoville & Milner 1957). H.M. was studied for 35 years after this operation, and the Hp has been associated with the formation of memories, and especially spatial memories (O'Keefe & Nadel 1978), ever since this (e.g. Corkin 2002).

Already in 1966, a Soviet scientist, Krushinskaya (1966), demonstrated that Eurasian nutcrackers use spatial memory to relocate caches and that they are dependent on an intact Hp for this. She allowed nutcrackers to store in an arena and then later to retrieve the cached nuts. She combined this design with surgical lesions of various parts of the brain. After Hp removal, a particular anomaly occurred that did not occur when other parts of the brain were operated on. The nutcrackers stored at normal intensities but could not relocate their caches during retrieval sessions. This study, of course, is a landmark among studies on memory in animals, but as Krushinskaya (1966) only published in Russian, it has not been as much cited as later studies. Her experiment has later been refined in two dimensions, the first being the 'spatial orientation relative to landmark's' part (Vander Wall 1982) and the second the 'Hp lesion design' part (Sherry & Vaccarino 1989).

6. THE EVOLUTION OF SCATTER HOARDING

(a) *Theoretical models*

Andersson & Krebs' (1978) game theoretical paper on the evolution of food hoarding has influenced many later studies. They identified some key conditions that must be fulfilled if a food-hoarding strategy should evolve within a species:

- (i) it must pay more to hoard than to leave the food for later consumption;
- (ii) it must pay more to hoard than to refrain from hoarding and instead scrounge on caches stored by other hoarders.

Condition (i) means that there must be fitness benefits from hoarding. I discuss some empirical studies that have explicitly shown that hoarding will increase fitness in §6b. Condition (ii) is typical game theory; Andersson & Krebs (1978) compared pay-offs for producers (hoarders) and scroungers (non-hoarders) in the same species, meaning that the players are competitors within the same gene pool. Regardless of whether cache loss is high or low, hoarding will be the ESS (evolutionary stable strategy) as long as hoarders do better than non-hoarders. At the time when this paper was published, rebuttal of group selection was a prime issue as arguments such as 'acting for the good of the species' or 'communal behaviour' was not uncommon in popular ornithological literature. For example, the largest Swedish daily newspaper 'Dagens Nyheter' used to publish popular notes about common birds. The hoarding behaviour in the coal tit was described as 'To guard itself against coming harsh times it spends most of the autumn doing advanced hoarding of spruce seeds... When cold weather arrives the individual birds will have rather hazy ideas on where they did cache. They eat willingly from caches made by other individuals. Every coal tit knows where food can be cached. Hence they visit such sites when they become hungry. The autumn hoarding is a collective behaviour aiming to save the species, not particular individuals'.

Haftorn (1956a, pp. 75–76) had a similar view that he described in his PhD thesis: 'The above remarks suggest the collective utilization of stored food, that is to say just the arrangement which would be most advantageous to the species'. Spruce seeds are primarily stored in spring, and he considered the fact that he found spruce seeds in the stomachs of yearlings as support of his view. He based this on the fact that yearlings could not yet possibly have experienced any spruce seeds storing when they were shot in winter.

Andersson & Krebs (1978) expressed condition (ii) above (that hoarding should pay more than cache pilfering) as

$$FH(nH) > FN(nH) \rightarrow p_s/p_o > (C/G)(n-1) + 1,$$

where $FH(nH)$ is the fitness of a hoarder in a group of n hoarders, $FN(nH)$ is the fitness of a non-hoarder in a group of hoarders, p_s is the probability that the hoarder relocates its cache, p_o the probability that another group member relocates it, C and G are the cost and gain of hoarding, and n is the group size.

Moreno *et al.* (1981) refined this equation and made it more testable by dividing p_s into two probabilities:

$$p_s = p_r + p_f.$$

Here p_r is the probability that a stored item remains in its cache (i.e. not pilfered or decayed) and p_f is the probability the hoarder can relocate its cache (for example, does not forget its location).

Smulders (1998) suggested that scatter hoarding under some circumstances can evolve under less strict conditions than the ones identified by Andersson & Krebs (1978). Many hoarding species (e.g. titmice and chickadees) live in stable, small groups of around four individuals (Ekman 1989). With no retrieval advantage for a hoarder and a cost of hoarding, it may seem obvious that the non-hoarders would be better off in a mixed group as a non-hoarder could share the benefits from hoarding but avoid the costs of it. However, a non-hoarding strategy would do very poorly in groups that mainly consist of non-hoarders. If hoarding is important for survival, individuals in pure groups of non-hoarders will have very low fitness. The high fitness of non-hoarders in our focal, mixed group will then be 'flooded' by the low average fitness of this genotype across all groups. It is the genotype non-hoarder that plays the game, and the fitness is calculated as an average across the whole field of players (Maynard Smith 1982).

Vander Wall & Jenkins (2003) suggested that hoarding could evolve despite high levels of pilfering. The rationale for making this model was the authors' observation that pilfering rates seem to be very high in many hoarding species. If pilfering is reciprocal between conspecifics, the loss to competitors could to some degree be compensated for by pilfering from these. Just as Smulders' (1998) model, this model proposes that hoarding can evolve under less strict conditions than suggested by Andersson & Krebs (1978). The model is a genetic algorithm with many factors and it is hard to see how scatter hoarding with high levels of reciprocal pilfering could occur in a simple

analytical model such as that of Andersson & Krebs (1978). The authors suggest that their system could be appropriate for rodents that use smell to locate caches. If a hoarder uses smell to locate scatter-hoarded caches, these can also easily be found by conspecific competitors. There is some support that reciprocal pilfering between hoarders could have a stabilizing effect in two later theoretical models that are based on desert rodent communities (Price & Mittler 2003, 2006).

Brodin *et al.* (2001) explored how much individuals of different dominance rank should invest in hoarding under various environmental conditions. The underlying assumption in this model was that dominants have free access to caches made by subordinate individuals, whereas subordinates cannot steal from dominants as easily. Under parameter values that are realistic, their model suggested that dominants in many cases should refrain from hoarding and instead steal caches made by subordinates (provided, of course, that they can locate such caches). The reason for this is that dominants in such cases can avoid the costs of hoarding (e.g. predation risk, energetic expenditure) in combination with 'forcing' subordinates to increase their storing effort. Subordinates are doing the best of a bad job. As they cannot gain anything by attacking dominants, they maximize fitness by storing sufficiently to hedge for pilfering from them.

(b) Empirical tests

The first take home message from Andersson & Krebs (1978) model is that there has to be a fitness benefit from hoarding. Otherwise, a food item could be left and eaten later. It is obvious that species which rely almost entirely on stored food for their winter sustenance could not survive without caches. The dependence on stored food is demonstrated by the irruptions that occur in many hoarding species when their preferred nut crop fails. One well-known example is the irregular massive migrations into Western Europe by the Siberian subspecies of the Eurasian nutcracker *N. c. macrorhynchus* during years when the Siberian stone pine *Pinus cembra sibirica* crop fails.

Still, there have been relatively few explicit demonstrations that scatter hoarding increases fitness. Grubb (1989) introduced a technique called ptilochronology, which literally means 'reading time in feathers'. Feathers display daily growth bars, a wide bar means that the feather has grown substantially on that day, a narrow bar means that it has grown less. If a tail feather, or rectrix, is removed in winter, replacement feathers will have especially clear growth bars (Brodin 1993b). Waite (1990) provided grey jays *Perisoreus canadensis* in some territories with substantial amounts of dog food pellets in autumn while jays in other territories were unsupplemented. After that, he stopped providing food, captured jays in both supplemented and unsupplemented territories and plucked one rectrix from each individual. In late winter, he recaptured these individuals and plucked the induced rectrices. Birds in the supplemented territories possessed wider growth bars than individuals from unsupplemented territories. This demonstrated that

supplemental food stored in autumn allowed them to stay in better conditions throughout the winter.

James & Verbeek (1984) showed that nest attentiveness increased in brooding female northwestern crows *Corvus caurinus* if their male partners were successful scatter hoarders. These crows store clams and other invertebrate prey that become available for a short period when the tide retreats. If storing has been successful, male crows can provide incubating females from the supply of stored food until the next retreating tide.

Wauters *et al.* (1995) demonstrated that scatter-hoarded food will increase survival in squirrels. Eurasian red squirrels *Sciurus vulgaris* that successfully retrieved many stored nuts increased body mass and winter survival compared with individuals that retrieved less.

The second important conclusion from Andersson & Krebs' (1978) model was that a strategy such as hoarding must pay better than a competing scrounger strategy. For scatter hoarders, this means that there must be a recovery advantage for hoarders in order for hoarding to remain as an ESS. A mixed strategy of the type suggested by Smulders (1998) could evolve with no hoarding advantage, but still remains to be demonstrated. The existence of a recovery advantage for hoarders is in many cases obvious. A hoarder that remembers the exact position of a cache will have a large advantage compared with a pilferer lacking such information. This means that hoarders that memorize caching locations almost by necessity will possess the necessary advantage.

Already, Swanberg's (1951) field observations provided strong support for the idea that Eurasian nutcrackers possess an accurate memory for caching locations. Krushinskaya's (1966) experiments verified this beyond doubt. Vander Wall (1982) elaborated her arena experiment with even clearer results in Clark's nutcracker.

However, there are other cases when a recovery advantage for hoarders is not obvious. For example, tits and chickadees will frequently retrieve stored items that they appear not to remember the precise locations of (Haftorn 1956a; Brodin 2005b). In cases when retrieval by memory is not obvious, a recovery advantage must be explicitly demonstrated to show that scatter hoarding is a stable strategy according to Andersson & Krebs (1978). Attempts to do this in the field have been made (i) with radioactively labelled seeds, (ii) with magnetic triggers and clocks and (iii) by tracing consumption of radioactively labelled food in the birds.

Cowie *et al.* (1981) labelled sunflower seeds with a strong gamma radiation emitter, technetium-99m, and provided these seeds to marsh tits in the field near Oxford, England. The marsh tits stored the labelled seeds around the feeder. The experimenters could then locate the cached seeds with a portable scintillation counter. The tits stored most seeds on the ground, under leaves, in moss, etc. For each seed that was located, Cowie *et al.* (1981) placed a control seed in a nearby similar location. The fact that cached seeds disappeared much quicker than control seeds suggests that hoarders remembered the

locations. However, this is not conclusive evidence of a recovery advantage as retrieval was not actually observed. For example, marsh tits could have cued in on some property of caching sites that the experimenters did not know of when they positioned control seeds. Such preferences could increase the disappearance rate of seeds stored by the birds compared with control seeds stored by humans. Brodin (1992) replicated this experiment on willow tits in coniferous forest in Sweden. Just as in the Oxford experiment on marsh tits, the cached seeds disappeared much faster than adjacent control seeds.

Stevens & Krebs (1985) developed a technique that aimed to specifically determine if seeds that disappeared from their caching locations had been recovered by the hoarder or stolen by a pilferer. At their field site near Oxford, marsh tits are territorial in pairs. In a number of pairs, they equipped one of the birds with a magnetic bird ring. They used the same technique as Cowie *et al.* (1981) and provided radioactively labelled nuts to the birds. When they observed the focal bird storing a nut, they identified the precise position with a portable scintillation counter. They then placed a magnetic sensor near each such cache. The sensors were connected to running clocks. The idea was that when the hoarder (with its magnetic ring) itself retrieved a cache, the magnetic sensor would be triggered and the clock would stop. If another bird (that lacked a magnetic ring) found the peanut, the cache would be emptied but the clock still running. The idea was good, but there were some technical problems. For example, clocks could stop even though the cache was still intact. The estimated 25 per cent recovery for hoarders they recorded is probably lower than the true recovery success.

Brodin (1993*b*) found a solution to these problems with a different approach. He developed a technique called radio-ptilochronology which consisted of provisioning of radioactively labelled food in combination with autoradiography of radioactive feathers. His technique made it possible to accurately follow the consumption of scatter-hoarded seeds in wild birds over long time periods. In a bird such as a willow tit, it will be possible to read around 35 daily growth bars from the top to the base of the feather. The replacement rectrix will start to emerge around 12 days after plucking. An induced rectrix will thus cover a time window of approximately 12–47 days after removal of the original feather.

Feather keratin is strong and durable, a property that is due to its di-sulphur bonds. This means that organic sulphur is in high demand during feather formation. Brodin (1993*b*) took advantage of this and labelled sunflower seeds with an amino acid containing a radioactive isotope of sulphur (^{35}S). When new feathers are under formation, organic sulphur will be directly incorporated in the part of the feather that is under formation.

Winter flocks of willow tits typically are small, territorial and resident. A week after removing a rectrix from each flock member, Brodin & Ekman (1994) provided 20 labelled sunflower seeds to one focal individual in each flock. The other flock members were

provided with the same number of unlabelled seeds. After two months had passed, the experimenters collected the replacement rectrices. Using autoradiography, they could then identify the parts of the feathers that contained radioactivity. By comparing this with the daily growth bars, they could follow consumption of labelled cached seeds in time. By comparing feathers from the focal bird with feathers from other flock members, they could also calculate cache pilfering rates. The hoarder's recovery advantage across the winter was around 5 : 1. Ekman *et al.* (1995) replicated this experiment on Siberian jays *Perisoreus infaustus* in Northern Sweden and found a recovery advantage of around 7 : 1. Clearly, hoarding may evolve under such conditions according to Andersson & Krebs (1978).

7. OPTIMAL SPACING OF CACHES AND THE DISPERSAL OF PLANTS BY SCATTER HOARDING ANIMALS

Optimal cache density and coevolution between plants and scatter hoarders may seem to be two different questions. However, the same year as Andersson & Krebs (1978) published their model, Stapanian & Smith (1978) published an influential model that treated both these subjects in the same theoretical setting. As the underlying assumption was that high cache densities will increase cache pilfering, their model is usually called the optimal (cache) density model. Stapanian & Smith (1978) investigated optimal cache spacing both from the squirrel's (it is optimal to minimize cache loss) and from the walnut's perspective (it is optimal to maximize sapling survival). This paper was special among scatter hoarding studies as it contained both a theoretical model and empirical tests of its predictions. Experiments on fox squirrels *Sciurus niger* scatter hoarding walnuts *Juglans nigra* provided the empirical data. The model can be summarized as a trade-off between costs of transporting caches away from the source and benefits from increasing their survival by decreasing cache density.

(a) *Optimal cache density*

One prediction from Stapanian & Smith's (1978) model was that as the area near a food source that is available for hoarding increased, the average distance to caches should decrease. The reason is that when a large area is suitable for storing close to the feeder, more caches can be made close to the feeder at a lower density. Another prediction was that if a food source becomes richer, transport distances should decrease so that caches are made closer to the source. The experimental tests showed that fox squirrels scattered caches close to the density that was optimal both for squirrels and for walnuts.

Stapanian & Smith's (1978) model was designed to find a specific, optimal density. Other authors have remarked that this may be less realistic; optimal cache density could, for example, decrease with distance from a central food source. Also, Clarkson *et al.* (1986) tested predictions from their model empirically, but on magpies *Pica pica* caching from bird feeders. As their model included transport time

and the optimization criterion was to maximize the amount of food stored, they predicted that optimal cache density should be highest around the food source and decrease with distance. This difference is not surprising as a basic assumption of Stapanian & Smith's (1978) model aimed to predict the average density across the whole caching area. Stapanian & Smith (1978) did not predict a constant density, they assumed it. In a system where squirrels store walnuts from trees that are evenly distributed over the forest, this may be a reasonable assumption. In a system when animals store food provided at a central source, an optimal cache density that changes with distance from the source may be more reasonable.

Kraus (1983) tested the optimal density model on Eastern grey squirrels *Sciurus carolinensis*. In his experiment, however, cache disappearance was so rapid that optimal density hardly could be calculated. He suggested that either cache disappearance must have been artificially low in Stapanian & Smith's (1978) experiment (because they wrapped walnuts in aluminium foil) or that the ecology of these two squirrel species must be different and that long-term hoarding may hardly occur in the Eastern grey squirrel.

Stapanian & Smith (1984) later refined their experiment in that they provided nuts from different plants, i.e. nuts that varied in nutritional value. Besides black walnuts, the fox squirrels could also store two species of acorns. As the walnuts are more valuable than the acorns, the prediction was that walnuts should be carried further away from a central source. The experiment supported this prediction. Hurly & Robertson (1987) tested the optimal density model on yet another squirrel species, the American red squirrel *Tamiasciurus hudsonicus*, and found that the squirrels transported whole peanuts longer distances than half peanuts before caching. However, as opposed to the optimal density model, but in agreement with Clarkson *et al.* (1986), they found that the density of caches changed with distance from the food source.

(b) *The dispersal of plants by scatter hoarding animals*

Scatter hoarders that bury caches in the ground may be important agents of seed dispersal. If such caching is beneficial both to hoarders and to plants, it is a form of symbiosis. Especially in cases when scatter hoarding birds or rodents specialize in one or a few plants species, such symbiosis may lead to coevolution. As this topic is thoroughly discussed in this issue by Vander Wall (2010), I will only mention it briefly here. Eurasian jays *Garrulus glandarius* store massive amounts of acorns from English oak *Quercus robur* acorns (Bossema 1979) and many acorns will not be recovered but left in the ground. Oak saplings are common in locations quite far from mature trees, and this phenomenon is usually attributed to dispersal by jays. Symbiosis of a similar type seems to exist between many hoarding animals and plants, for example, the Eurasian nutcracker and hazel (e.g. Swanberg 1951) (or in some areas between these

birds and stone pine), blue jays *Cyanocitta cristata* and pin oak *Quercus palustris* (Darley-Hill & Johnson 1981), and Clark's nutcracker and whitebark pine *Pinus albicaulis* (Tomback 1982). In fact, not less than 20 species of pines seem to be dependent on dispersal by one of the two nutcracker species (Tomback & Linhart 1990).

8. MODERN ORNITHOLOGICAL FIELD STUDIES

By field studies, I mean the type of studies that Haftorn (1956b, 1959) and Swanberg (1951, 1956) did, observing birds foraging naturally, as opposed to field experiments when storable food is provided at feeders. Modern field studies on scatter hoarding differ from older ones in several respects. First, the subjects have been individually colour-banded birds, a necessity for identifying individuals in most species. This is a pre-requisite for objective sampling of behaviour, in most cases also for statistical testing. Second, data are collected with standardized observation methods, for example pre-determined observation intervals. This reduces the risk that behaviour which is easy to observe, such as scatter hoarding, is overestimated. It also makes data more independent as 'easy-to-observe' individuals are not followed for long periods. Third, hypotheses are tested statistically. Finally, data have in many cases been collected to answer specific questions whereas Swanberg's (1951) and Haftorn's (1956b) studies were descriptive, driven by a general ornithological interest.

Pravosudov (1985, 1986) recorded scatter hoarding behaviour in willow and Siberian tits *Parus cinctus* in the White Sea region, Russia. During a spruce mast year, he recorded the highest hoarding rates ever reported, around 460 000 stored items per individual and year in willow tits, and over 500 000 items per individual and year in Siberian tits.

He also discovered that there were significant differences in hoarding niches, not only between the two species, but also between conspecifics within a flock. Individually separated niches will increase the probability that a hoarder can retrieve its own caches and thus increase the stability of a hoarding strategy according to Andersson & Krebs (1978).

Brodin (1994c) examined hoarding behaviour in willow tits near Stockholm in Sweden. Hoarding rates were quite similar to the ones reported by Haftorn from the same latitudes in Norway, around 40 000–60 000 items per individual in one autumn. Haftorn's reports of long-term hoarding in titmice had been challenged by discoveries in Oxford that marsh tit caches were retrieved or pilfered within a day or two after storing. The marsh tit is a close relative to the willow tit, the essential ecological difference being its preference for deciduous forest. Brodin (1993a) showed that the contradictory results depended on the fact that caches were concentrated at high densities around feeders. Nuts cached by willow tits from feeders had almost exactly the same disappearance rates as for marsh tits, whereas naturally made caches may last for months. This makes sense in the light of optimal cache density theory; natural caches are scattered across a large winter territory

whereas seeds provided at a feeder essentially will be concentrated within 50 m radius of a feeder.

In another experiment, Brodin (1994a) rebaited caches from which seeds had already been removed by the birds. As most of these must have been retrieved by the hoarders (Brodin & Ekman 1994), he could in this way estimate the cache disappearance rate owing to other factors, i.e. cache loss. The reason is that hoarders remember which caches they have emptied and do not revisit such sites (Sherry 1982, 1984). The total loss was low, around 1.3 per cent per day. The high pilfering rates reported for marsh tits (Cowie *et al.* 1981) (most control seeds disappeared within 20 daylight hours) thus appear to be an effect of the high concentration of food around feeders. Finally, Brodin (1994b) confirmed the discovery made by Pravosudov (1986) that hoarding niches in willow tits will differ between conspecific members of the same flock. The habitat separation was a function of dominance rank, where dominant individuals preferred to forage higher up in the trees.

Lens *et al.* (1994) investigated natural hoarding in crested tits. They discovered an intraspecific separation of caching niches also in this species. Just as in willow tits, the driving factor seemed to be dominance rank.

9. THE NATURE OF CACHING MEMORY

Memory in scatter hoarding birds has become an established system for memory studies in an evolutionary framework. The first studies were confirmations of Krushinskaya's (1966) report that spatial memory was used to relocate caches. Later studies have diverged in several directions: (i) exploration of the specific nature of the spatial memory systems that are involved, (ii) exploration of involvement of the Hp and (iii) studies of spatial memory in relation to Hp morphology. Most studies in the field have been laboratory experiments, but there are also a number of reviews on this topic (Shettleworth 1995; Shettleworth & Hampton 1998; Balda & Kamil 2006 on American corvids).

In a well-designed elaboration of Krushinskaya's (1966) arena experiment, Vander Wall (1982) demonstrated that landmarks are crucial for cache recovery in nutcrackers. He allowed Clark's nutcrackers to store in an arena filled with sand. In one of his experiments, he had covered the arena with a plastic sheet that was open only in an oval in the centre of the aviary where the ground was accessible for storing. On top of the sand, he had placed stones, logs, etc. as landmarks. Before retrieval sessions, he elongated one end of the oval and moved the landmarks in this end in the same direction the same distance. In the other, not manipulated end, the landmarks were left in their original positions. There were no landmarks in the centre of the oval, only at the ends. When the nutcrackers searched for cached nuts at the manipulated end of the arena, they missed their caches with a distance corresponding to the elongation of the arena. In the undisturbed end, the nutcrackers relocated caches accurately. In the central part of the arena, the nutcrackers missed their caches with about half the distance of the manipulation. This suggests

that the birds estimated caching locations here by interpolation of landmark positions from both ends.

In an elegant experiment, Sherry *et al.* (1981) demonstrated that spatial memory impressions from one eye are stored in the contralateral part of the brain. They allowed captive marsh tits to store with a plastic non-transparent cup glued over one eye. If the cup was transferred to the other eye before the retrieval session, the birds' retrieval performance was at random chance levels. If the cup was left on the same eye, they retrieved with high, normal success. The clever insight behind this design was the fact that animals with laterally placed eyes, like most song birds, have a complete crossing of the optic nerves at the chiasma. This means that all information from the left eye is stored in the right brain hemisphere and vice versa. Animals with frontally directed eyes, on the other hand, have an incomplete optic nerve crossing in order to coordinate stereoscopic vision.

In two experiments, Shettleworth & Krebs (1982, 1986) further explored the nature of the avian caching memory, using black-capped chickadees and marsh tits. In the first, they showed that besides spatial memory for caching locations, the birds possessed clear preferences for certain sites. It has later been demonstrated that such preferences may occur on a general species level, as well as being more specific for individual hoarders (Brodin & Kunz 1997). Such preferences facilitate retrieval of caches that have been forgotten. In the second study, Shettleworth & Krebs (1982, 1986) compared how successfully the birds could retrieve caches they had made themselves compared with food that they could observe through small plastic windows. The bird retrieved seeds observed during 'window shopping' better than expected by chance, but were not as successful as when they retrieved own caches.

Baker *et al.* (1988) showed that black-capped chickadees perching in a small cage inside an aviary were not able to memorize caching locations they observed other birds to use. Corvids, such as pinyon jays *Gymnorhinus cyanocephalus*, on the other hand, possess such observational memory (Bednekoff & Balda 1996; Balda & Kamil 2006). Another corvid, the scrub jay *Aphelocoma californica* has been demonstrated to also remember not only positions, but also contents of caches (Clayton & Dickinson 1999). As the scrub jay is considered not to be a highly specialized hoarder (see §10b for a definition of this term), it is probable that most scatter hoarding birds have this ability. For example, to some extent, it has been demonstrated in black-capped chickadees, and as previously mentioned these have been demonstrated to remember whether caches have been retrieved (Sherry 1982, 1984).

Krebs *et al.* (1990) used the window-shopping design to compare memory for locations of observed (but not cached) seeds in hoarding coal tits with memory performance in their non-hoarding relative, the great tit *Parus major*. Differences were small, suggesting that great tits were equally good as coal tits on this spatial memory task. Clayton & Krebs (1994) and Brodbeck (1994) showed that hoarding species seem to prefer spatial cues over object-specific ones, whereas there was no preference of this sort in non-hoarding species.

Besides the ability to remember a large number of caching locations, highly specialized scatter hoarders are believed to have long-lasting memories. Balda & Kamil (1992) allowed captive Clark's nutcrackers to retrieve caches after various long retention intervals. There was some evidence for an impaired performance after the longest interval, 285 days, but overall the birds still appeared to remember caching locations accurately. Parids do not appear to possess such an impressive long-term memory. Black-capped chickadees and willow tits retrieved accurately shortly after storing, but retrieval performance decayed gradually to the same levels as retrieval of control seeds four weeks after storing (Hitchcock & Sherry 1990; Brodin & Kunz 1997).

Although studies on spatial memory in scatter hoarding animals have focussed on birds, there have also been some studies on mammals. Frequently, mammals will retrieve caches by their smell, and it has been discussed whether they are able to use spatial memory in the same way as birds for this. By comparing the ability of Eastern grey squirrels to relocate own caches with their ability to find nearby caches made by other squirrels, Jacobs & Liman (1991) could demonstrate that these squirrels are able to use memory for cache retrieval.

10. SPATIAL MEMORY CAPACITY AND HP VOLUME

I will discuss some particular aspects of the relationship of hoarding to Hp volume. However, a broader discussion of this topic is provided in this issue by Roth *et al.* (2010). They point out that even though Hp volume has historically been a key variable in this research, other properties of the Hp may be more relevant as physiological correlates of memory capacity.

(a) Family level comparisons

According to a 'the bigger the better' idea (for a more nuanced discussion of this, see Jerison (1973) and Striedter (2005)), one could hypothesize that scatter hoarders should possess larger Hp than non-hoarders as they need to memorize more locations. In 1989, two influential papers were published that compared Hp volume in passerine families of hoarding species with families of non-hoarding species (Krebs *et al.* 1989; Sherry *et al.* 1989). Both studies showed that families of hoarding species possess significantly larger Hp than families of non-hoarding ones. However, the resolution of these studies was coarse for several reasons: (i) the phylogenetical level was high as families were compared, (ii) the resolution of the independent variable, hoarders or non-hoarders, is poor and (iii) the parids and corvids contain both hoarding and non-hoarding species and these families were divided into non-existing subfamilies according to this categorization. Hampton & Shettleworth (1996) showed that Hp lesions specifically will affect spatial memory but not memory for colour both in the hoarding black-capped chickadee and in the non-hoarding dark-eyed junco, *Junco hyemalis*.

It can be argued that the evidence that a relatively larger Hp is an adaptation for scatter hoarding,

rather than for something else, will be stronger the more closely related the taxa under comparison are. It will be easier to identify ecological factors that cause a difference between populations of the same species than the factors that cause differences between families. The discovery that families of hoarders possess larger Hp than families of non-hoarders (Krebs *et al.* 1989; Sherry *et al.* 1989) could thus be seen as a suggestion in which direction we should go, whereas an intraspecific effect of hoarding propensity on Hp volume in black-capped chickadees (Roth & Pravosudov 2009) is stronger evidence. Populations within a species will differ mainly in adaptations to local conditions that we can observe today, whereas families diverged a long time ago and hence may differ for unknown historical reasons.

(b) Species level comparisons

Healy & Krebs (1992, 1996) introduced a three-category rank scale: non-hoarders, hoarders of intermediate specialization and highly specialized hoarders. Healy and Krebs found that relative Hp volume increased with hoarding propensity in both corvids and parids. Hampton *et al.* (1995) found support for such an increase in three species of American parids. There are also studies, however, that have failed to find a correlation in species level comparisons. Volman *et al.* (1997) found no tendency towards a correlation in three species of American woodpeckers. Brodin & Lundborg (2003) measured Hp volume in four species, pooling all available data, but found no correlation despite their large dataset. Somewhat surprisingly, Lucas *et al.* (2004) found that a correlation reappears if continent is controlled for. In this dataset, American species on average possess 10 per cent smaller Hp than Eurasian species. I do not know of any factor that could create such a difference and it is likely that it depends on methodological differences between laboratories (see Roth *et al.* 2010).

(c) Intraspecific comparisons

Pravosudov & Clayton (2002) and Roth & Pravosudov (2009) showed that black-capped chickadees from regions with harsher winter climates store more food and possess larger Hp than individuals from regions with milder winters. The reason is that birds from regions with harsher winters need more stored food and thus should specialize more in hoarding.

Such a correlation could have developed gradually over evolutionary time as the ancestors of today's specialist scatter hoarders developed this behaviour. Alternatively, an enlargement of the Hp could be plastic and induced within the individual hoarder by hoarding activity. In such a case, some individuals in a species that store a lot could possess a larger Hp than individuals that store less. Hp volume may even vary within individuals so that it increases in autumn when hoarding is intensive and decreases at other times of year.

(d) Induced Hp growth

Barnea & Nottebohm (1994) studied at what rate new neurons were incorporated in the Hp of black-capped

chickadees in the field. They found that the rate increased by 0.2–0.3% in autumn, the season when hoarding intensity peaks in this species (Brodin 2005a). Even though it has long been known to the scientific community that neurogenesis occurs not only in juveniles but also in adults, this paper received much public attention, making it into the headlines of several large newspapers across the world.

Even if the seasonal variation in neurogenesis rate was only around 0.3 per cent, this discovery provides a possible mechanism for usage-induced variation in Hp volume. Another discovery that addresses individually induced changes in Hp volume was made by Healy *et al.* (1994), who showed that the Hp grows for a relatively longer time in hoarding marsh tits than in non-hoarding blue tits *Cyanistes caeruleus*. Whether there can be induced growth of gross Hp volume also in adult individuals is less clear. The best way to verify such an effect would be to measure Hp volume repeatedly in living birds, for example, at different times of year. As this is not yet possible, the technique has been to compare birds that have been sacrificed at different seasons. Smulders *et al.* (1995) found that Hp volume in wild black-capped chickadees was slightly larger in autumn, when hoarding intensity peaks (Brodin 2005a), than at other times of the year. There have been attempts to replicate such an effect, but so far with little success (Krebs *et al.* 1995; Cristol 1996; Macdougall-Shackleton *et al.* 2003; Hoshooey *et al.* 2006).

(e) *The neuroecology debate*

Bolhuis & Macphail (2001) launched a massive criticism to the comparative approach in studies of the correlation between hoarding specialization and Hp volume. Invoking Tinbergen's (1963) four levels of explanation, they proposed that the neuroecological (ecology in this context means 'evolutionary') approach was flawed and that these types of comparative studies were not valid. Furthermore, they suggested that data supporting this correlation were weak or even negative. This spurred an animated debate between proponents (Dwyer & Clayton 2002; Hampton *et al.* 2002; Healy *et al.* 2005) and opponents (Bolhuis & Macphail 2002; Francis 2005) of this type of studies. For a recent review of this topic, see Sherry (2006). In my own view, some of Bolhuis & Macphail's (2002) criticism may have been correct in that some studies may have been 'over adaptationistic' but that the field at large has provided valuable insights into spatial memory and its neural correlates (e.g. Brodin & Bolhuis 2008).

11. CONCLUSIONS

Scatter hoarding behaviour in animals has been known for a long time. Scientific studies of this behaviour have developed from simple, naturalistic field studies into modern up-to-date studies in several fields. The demonstration by Krushinskaya (1966) that a specific part of the brain, the Hp, was important for caching memory storage in Eurasian nutcrackers spurred a number of studies on scatter hoarders, spatial memory and the Hp. Most of these have been on

birds, and this has now become the prime study system for evolutionary studies of spatial memory. There have also been some studies on mammals on this topic, but in general their caching behaviour has not been as well studied as that of birds.

The focus on many studies has been on the Hp in relation to spatial memory capacity. Even if such a correlation has been criticized, evidence suggests that such a correlation exists and that it has developed over evolutionary time, with scatter hoarding species possessing more specialized Hp than non-hoarders. It is still an open question whether frequent spatial memory use (high rate caching and memorization) induces Hp growth within individuals.

This study system has branched into neighbouring disciplines that are beyond the scope of a historical review of scatter hoarding. Examples of these are studies on cognitive abilities in birds (e.g. Griffiths *et al.* 1999; Emery *et al.* 2003) and studies on cognition and the brain in general (e.g. Healy & Rowe 2007).

The publication of Andersson & Krebs (1978) game theoretical paper that pointed out the conditions under which scatter hoarding could evolve was the starting point for a number of theoretical and behavioural studies on the evolution of hoarding as strategy. A basic condition is the existence of a recovery advantage for hoarders compared with pilferers. Such an advantage can be provided, for example, by an accurate memory for caching locations. Most studies confirm the existence of such an advantage.

A high concentration of cached food in a small area could attract cache pilferers. Stapanian & Smith's (1978) theoretical and empirical study of scatter hoarding squirrels predicted that caching density should be optimized to minimize cache loss. Later studies have showed that it may be important to also include transport distance from the food source in the optimization criterion. Stapanian & Smith (1978) also realized that scatter hoarding animals may be important dispersers of plants and that scatter hoarding in this way could be beneficial to the plant. Thus, scatter hoarding animals and the plants they disperse could be a case of symbiosis and, possibly, coevolution.

The scatter hoarding paradigm has been an integrative meeting point for ethology, behavioural ecology, evolutionary psychology, memory psychology and memory morphology/physiology. Even if some comparative studies on memory and Hp volume have been criticized, the field seems to be more vivid than ever.

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