

1 **Title**

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3 Hyper-dispersed cache distributions reduce pilferage: A field study

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1 Many animals hoard food when it is plentiful for periods when it is scarce. The time
2 between storage and retrieval can be a matter of hours to months. To increase the
3 probability that their hoards will still be available when needed, hoarding should
4 happen in such a way that it reduces cache loss. Scatter hoarders can do this by
5 manipulating the density and dispersal of caches to minimize the foraging efficiency
6 of pilferers. Previous work has shown that there is an optimal density which reduces
7 cache loss. This study investigates whether cache distribution patterns can be
8 manipulated to reduce cache loss. Seeds were distributed in a uniform, random or
9 clustered manner in the field and their survival was tested. More hyper-dispersed
10 distributions reduced seed loss indicating that these distributions may be useful to
11 hoarding animals. The most clustered distributions of seeds became more hyper-
12 dispersed as time progressed, decreasing the risk of discovery for the remaining
13 caches. This suggests that hoarders could adopt the alternative strategy of hoarding a
14 larger number of items to begin with, allowing initial cache loss to gradually produce
15 a more hyper-dispersed distribution as the clustered sections are removed. Further
16 work needs to investigate whether it is evolutionarily adaptive to invest in hoarding
17 more items, or to invest in a hyper-dispersing strategy. Our results also show that
18 seeds disappeared at a lower rate in the winter, suggesting there is some degree of
19 safety for hoarded food when it is needed most.

20

21

1 For hoarding to be adaptive, the hoarder should not only increase the odds of
2 retrieving its own caches (Andersson & Krebs 1978) but also minimize the chances of
3 other animals finding them first (Smulders 1998). Strategies for the former, such as
4 memory-based retrieval, have been suggested (Cowie et al. 1981; Sherry et al. 1981;
5 Sherry et al. 1982; Sherry 1982; Shettleworth & Krebs 1982; Shettleworth 1983;
6 Sherry 1984a; Sherry 1984b). Here, we focus on strategies to reduce cache loss. Some
7 species store food in a single large cache or a very concentrated area in an animal's
8 home range (larder hoarding), devoting considerable time to aggressive defence as the
9 larder is particularly attractive to potential cache thieves (Vander Wall 1990). Other
10 species disperse their caches across their home range (scatter hoarding), thus
11 spreading the risk of cache loss (Vander Wall 1990). Rodents and perching birds, such
12 as parids and corvids, are well-known scatter hoarders (Vander Wall 1990). Scatter
13 hoarders have evolved a range of strategies to reduce cache loss; for example, when
14 hoarding food, willow tits (*Parus montanus*) (Lahti & Rytkonen 1996), coal tits
15 (*Parus ater*) (Brotons 2000), nuthatches (*Sitta europaea*) (Carrascal & Moreno 1993),
16 European jays (*Garrulus glandarius*) (Bossema 1979), gray jays (*Perisoreus*
17 *canadensis*) (Burnell & Tomback 1985) and ravens (*Corvus corax*) (Bugnyar &
18 Kotrschal 2002) avoid storing in the presence of conspecifics or heterospecifics. Also,
19 different species use different hoarding sites (Haftorn 1956; Pravosudov 1986). In
20 particular, willow tits minimize heterospecific pilferage when foraging in mixed
21 species flocks by avoiding using the same type of hoarding location as other species
22 (as shown in mixed flocks with crested tits (*Parus cristatus*) (Suhonen & Alatalo
23 1991) and with Siberian tits (*Parus cinctus*) (Alatalo & Carlson 1987)). Similarly,
24 intraspecific pilferage is minimized by the rank-dependent sub-division of hoarding
25 sites on trees in willow tits (Brodin 1994a) and crested tits (Lens et al. 1994).

1 For scatter hoarders, there are different aspects of the cache distribution that
2 can be manipulated to further reduce cache loss. It has already been shown that
3 animals hoard food at a particular density to reduce cache loss (Stapanian & Smith
4 1978; Sherry et al. 1982; Stapanian & Smith 1984; Waite 1988). In two separate
5 studies using fox squirrels (*Sciurus niger*) and black walnuts (*Juglans nigra*) buried in
6 grids with different nearest neighbour distances, Stapanian and Smith (1978, 1984)
7 showed that the mean time of survival of buried nuts tends to decrease with increasing
8 density of buried nuts. In a similar study using sunflower seeds, Sherry et al. (1982)
9 found that there was an optimal density (~7m nearest neighbour distance) for the
10 survival of simulated marsh tit (*Parus palustris*) caches. While these studies looked at
11 the effect of density in regular grids, there have been few studies which consider
12 whether there is a *type* of distribution (or local density pattern) which reduces cache
13 loss. Theoretically, an animal may hoard its caches at the same average density in a
14 clustered distribution (the presence of one point increasing the probability of finding
15 another nearby), a random distribution (the points occurring independently of each
16 other) or a uniform distribution (the presence of one point decreasing the probability
17 of finding another nearby) (Dale 1999). Studies of the distribution of food or prey
18 items suggest that most animals forage more efficiently on clumped resources than on
19 hyper-dispersed ones (Ivlev 1961; Emlen 1973; Reichman & Oberstein 1977;
20 Reichman 1979; Laca 1998), which is consistent with the fact that insect, bird and
21 mammalian foragers generally use area-restricted searching tactics (Tinbergen et al.
22 1967; Stapanian & Smith 1978; Traniello et al. 1991; Benedix 1993; Dejean &
23 Benhamou 1993; Keasar et al. 1996; Withers & Harris 1996; Munyaneza & Obrycki
24 1998; Hill et al. 2000; Lode 2000; Leising 2001; Leising & Franks 2002).
25 Theoretically, foraging efficiency should be the lowest in random distributions as they

1 give the foragers the least information about the whereabouts of other food items.
2 However, because random distributions contain some clusters, we predict that a more
3 hyper-dispersed distribution should reduce foraging efficiency below that obtained in
4 a random distribution and could be used by scatter hoarders to reduce cache loss. As
5 further investigations of possible cache distributions have been encouraged (Jenkins et
6 al. 1995), this study aims to test this hypothesis by comparing the survival of food
7 items in four different distributions in the field.

METHODS

Procedure

The experiment was performed in Gosforth Nature Reserve (Lat: 55:01:38N Lon: 1:35:42W), which consists of mixed deciduous and coniferous woodland. A number of seed-eating birds are commonly found within the Reserve (Hammock & Noble-Rollin 1990), including the coal tit (*Parus ater*), blue tit (*Parus caeruleus*), great tit (*Parus major*), long-tailed tit (*Aegithalos caudatus*), marsh tit (*Parus palustris*), willow tit (*Parus montanus*), nuthatch (*Sitta europaea*), Eurasian jay (*Garrulus glandarius*), chaffinch (*Fringilla coelebs*), greenfinch (*Carduelis chloris*), goldfinch (*Carduelis carduelis*), siskin (*Carduelis spinus*), bullfinch (*Pyrrhula pyrrhula*), wood pigeon (*Columba palumbus*), greater spotted woodpecker (*Dendrocopos major*), dunnock (*Prunella modularis*) and robin (*Erithacus rubecula*). Our artificial cache distributions were similar to those generated by Sherry et al. (1982) except that ours manipulated distribution rather than density. Four different artificial cache distributions were created, each containing 25 halved, husked sunflower seeds. Distributions were laid out in four different 50m x 50m plots, which were separated from each other by at least 50m, as in Sherry et al. (1982). Plots were positioned in areas with dense vegetation so that there were a high number of possible cache sites. The average nearest neighbour distance between seeds was 7m in each distribution as this is the optimal density which reduced cache loss for marsh tits (*Parus palustris*) (Sherry et al. 1982). Nearest neighbour distance was used in this study as we considered it the most relevant measure from the point of view of a forager. Each distribution was tested in each plot once in the autumn and again in the

1 winter (in 4 trials between 20 October and 13 November 2003 and then again 4 trials
2 between 3 February and 5 March 2004). The order of treatments was balanced across
3 plots and trials, in a Latin square design, so that at any point in time, each distribution
4 was represented.

5
6 Four distributions were used: one uniform, two random and one clustered (Fig.
7 1). The artificial caches could, in theory, be at any location in the 50m (x axis) by
8 50m (y axis) grid providing that the co-ordinates were whole integers. The ‘uniform’
9 distribution was laid out in a square grid, as tested previously (Sherry et al. 1982). The
10 two quasi random distributions (which were constrained by an average nearest
11 neighbour distance of 7m) consisted of 25 randomly generated x and y co-ordinates.
12 Two distributions were used: one with low variability in nearest neighbour distance
13 (‘Random (Low)’) and one with high variability in nearest neighbour distance
14 (‘Random (High)’). The ‘clustered’ distribution consisted of five clusters of five
15 seeds, each separated from the others in the cluster by 0.5m. In the case of the
16 clustered distribution, the nearest neighbour distance was defined as the minimum
17 distance between a seed in one cluster and a seed in a neighbouring cluster. The
18 clusters themselves were distributed randomly across the plot.

19
20 As previous experiments have shown that the disappearance of caches is
21 dependent on the type of cache site (Sherry et al. 1982), a fixed number of different
22 site types were used in each distribution. When distributions were set up in a
23 preliminary experiment, it appeared that trees were only present in approximately 10
24 to 15 out of 25 co-ordinates within each plot. Therefore, in each distribution, 10 sites
25 were on tree trunks, 10 were near the ground (on logs, in ferns, etc, but never on the

1 ground), and 5 were in branches. The vegetation cover was relatively dense at the
2 study site so there was usually an appropriate type of cache site (e.g. tree trunk, near
3 ground or branches) at the pre-determined cache co-ordinates. The occurrence of type
4 of cache site therefore did not normally constrain cache distribution. However, on the
5 occasions when an appropriate cache site was unavailable at the specified cache co-
6 ordinates, the seed was cached at within 50cm of the desired co-ordinate. Our cache
7 sites were close to the ground, as in Sherry et al. (1982), so cache heights varied
8 between 0.1m and 1.5m. Each cache site was labelled with a numbered tag (1 to 25),
9 positioned at a distance of at least 1m from the cache site. Coloured ribbon was also
10 tied to a nearby branch, typically in a different direction to the label and again at least
11 1m from the cache site. Detailed descriptions of each cache site were recorded noting
12 the locations of the tag and ribbon relative to the seed. Any distinguishing features
13 (e.g. nearby branches, twigs, vegetation) were noted and a digital photograph was
14 taken of the cache site to aid recovery.

15

16 After the set up of the distributions on Day 0, cache loss was recorded by
17 checking the presence or absence of seeds once in the morning and once in the
18 evening each day for three days (Days 1, 2 and 3), providing data for 6 time points
19 after set-up. The morning and evening checks were timed so that the experimenter
20 entered or left Gosforth Nature Reserve as the sun was rising or setting respectively.
21 One such three-day session represents one trial. At the end of Day 3, all the remaining
22 seeds were removed and the sites were left for three days before the next trial. Each
23 new trial was started on the same day of the week and there were four trials in each
24 season. On occasions, the seeds were not completely removed by the foragers i.e. a
25 few fragments remained or the seed had uneven edges. If approximately over 50% of

1 the seed had been removed, it was recorded as 'disappeared' and any remaining
2 fragments were removed. If the majority of the seed remained, it was recorded as 'not
3 disappeared' and the seed was left in its cache site. The general weather conditions
4 (maximum and minimum temperature, precipitation and snow) were recorded each
5 day to determine their effect on the disappearance of caches.

6

7 **Analysis**

8

9 A continuous measure of distribution (i.e. a dispersal measure) was calculated
10 for all distributions of seeds at each 'time interval' (i.e. each time seeds were
11 checked). To calculate these dispersal measures, the 50m by 50m plots were divided
12 into quadrats of 10m by 10m, quadrat counts of seeds were taken and the average
13 mean and variance of quadrat counts was calculated. Various dispersal measures have
14 been devised which explore the relationship between the mean and variance of
15 quadrat counts because distribution is a function of the variance. After consideration
16 of Upton and Fingleton's (1985) comprehensive review of the various dispersal
17 measures, the Index of Dispersion ($ID = (n-1)s^2/\bar{x}$ where n is the number of quadrats, s^2
18 is the variance of quadrat counts and \bar{x} is the mean of quadrat counts) (Hoel 1943)
19 was used in this analysis. A high ID indicates that the distribution is clustered whereas
20 a low ID indicates that it is hyper-dispersed.

21

22 The statistical package SPSS for Windows Version 11.0.0 was used for the
23 statistical analysis. All data were normally distributed unless stated otherwise. In
24 general, repeated measures ANOVAs were used to analyse the data with trial as the
25 unit of analysis. Distribution and time (the six timepoints at which seed presence was

1 checked) were within-trial variables and season was a between-trial variable.
2 However, for the average daily temperature analysis, time interval was the unit of
3 analysis, distribution was a within-unit variable and season and time were between-
4 unit variables. This was necessary because temperature readings were available for
5 each day rather than each trial (three days). Using RM ANOVA is mathematically
6 identical to a General Linear Model ANOVA with time and distribution nested within
7 trial, season as a fixed effect and trial as a random effect. Logistic regression was
8 used to analyse the height of seeds which disappeared in the day and night and each
9 seed was considered as an independent data point. Results were considered significant
10 if $p < 0.05$.

RESULTS

Number of seeds remaining

The number of seeds remaining decreased with time since set up (RM ANOVA: $F_{5,192}=51.220$, $P<0.001$) and fewer seeds disappeared in the winter compared with the autumn (RM ANOVA: $F_{1,192}=15.843$, $P=0.007$). After 3 days, there was an average of 56% of the artificial caches remaining in the most hyper-dispersed distribution whereas there was only an average of 40% remaining in the most clustered. Statistical analyses reflect this difference as there was an effect of distribution on the number of seeds remaining (RM ANOVA: $F_{3,192}=5.318$, $P=0.008$) (Fig. 2). Post hoc analysis shows that fewer seeds disappeared in the Uniform distribution than in the Clustered (RM ANOVA: $F_{1,96}=13.432$, $P=0.011$) and Random (High) (RM ANOVA: $F_{1,96}=17.128$, $P=0.006$) distributions, and fewer disappeared also in the Random (Low) than in the Clustered distribution (RM ANOVA: $F_{1,96}=6.776$, $P=0.040$). There was no effect of height on whether or not a seed disappeared, but the trend suggested that lower seeds were more likely to disappear (Logistic regression: $Wald_{1,800}=3.390$, $P=0.066$). Also, seeds that disappeared during the day were higher than those that disappeared at night (Logistic regression: $Wald_{1,418}=4.186$, $P=0.041$). It is unlikely that the effect of distribution was a result of different distributions having seeds at different heights because there were no differences in average height among the distributions (RM ANOVA: $F_{3,32}=2.339$, $P=0.108$). Sites generated in the winter were lower than those in the autumn (RM ANOVA: $F_{1,32}=8.672$, $P=0.026$). However, this cannot explain the effect of season on disappearance, since the effect goes in the opposite direction.

1 When average daily temperature was included as a co-variate, with
2 distribution as a within-subject variable and time interval and season as between-
3 subject variables, more seeds disappeared at higher temperatures (RM ANOVA:
4 $F_{1,192}=6.280, P=0.017$). There was an effect of distribution (RM ANOVA:
5 $F_{3,192}=2.690, P=0.050$) and more seeds disappeared in the autumn than in the winter
6 (RM ANOVA: $F_{1,192}=31.218, P<0.001$). This analysis indicates that temperature
7 acted independently of season because, even when statistically controlling for season,
8 there was an additional effect of temperature on the number of seeds that disappeared.

9

10 When presence or absence of snow in the four-day period (set up and
11 observational days) was scored and included as a factor (there was snow during two
12 out of the four trials of winter) and season was also included as a between-trial
13 variable, the trend suggests that snow cover reduced seed loss (RM ANOVA:
14 $F_{1,192}=6.197, P=0.055$). Again, there was an effect of distribution (RM ANOVA:
15 $F_{3,192}=5.054, P=0.013$) and more seeds disappeared in the autumn than in the winter
16 (RM ANOVA: $F_{1,192}=6.197, P=0.030$). This indicates that the effect of season is not
17 purely due to there being snow cover in winter, because, even when statistically
18 controlling for snow cover, fewer seeds still disappeared in the winter.

19

20 **Rate of disappearance**

21

22 Figure 2 suggests that the rate of disappearance of seeds may have differed
23 among distributions. Therefore, the rate of disappearance for different distributions
24 over time was calculated as follows:

25

$$\% \text{ of seeds disappeared per hour} = \frac{\left(\frac{\text{number of seeds that disappeared since the last time interval}}{\text{number of seeds remaining at the last time interval}} \times 100 \right)}{\text{the number of hours since the last time interval}}$$

1
2 The data were significantly different from normal (Kolmogorov-Smirnov: $Z_{192}=3.353$,
3 $P<0.001$) but transformations, such as log (Kolmogorov-Smirnov: $Z_{192}=3.784$,
4 $P<0.001$), ln (Kolmogorov-Smirnov: $Z_{192}=3.784$, $P<0.001$), square root
5 (Kolmogorov-Smirnov: $Z_{192}=3.984$, $P<0.001$) and arcsine square root (Kolmogorov-
6 Smirnov: $Z_{192}=3.979$, $P<0.001$) made the data more different rather than less different
7 from normal. Untransformed data were therefore used in the analysis, because
8 ANOVAs are notoriously robust to deviations from normality. Disappearance rates
9 were higher during the night than during the day (RM ANOVA: $F_{1,192}=16.792$,
10 $P=0.006$), but there was no main effect of day (1-3) (RM ANOVA: $F_{2,192}=3.354$,
11 $P=0.070$). There was also no effect of distribution (RM ANOVA: $F_{3,192}=0.382$,
12 $P=0.767$) as implied by the raw data: in the most hyper-dispersed distribution, an
13 average of 1.02% of seeds disappeared per hour and, in the most clustered
14 distribution, an average of 1.16% of seeds disappeared per hour. No main effect of
15 distribution on disappearance rates is interesting given that there were differences
16 between distributions in the number of seeds remaining (see above). There was
17 however a significant interaction between distribution and time of day ($F_{3,192}=3.385$,
18 $P=0.041$), with the disappearance rates being higher in the more clustered
19 distributions at night, but not during the day (see below for a more detailed
20 breakdown). This suggests that the effect seen in the first analysis is probably due to
21 the difference in disappearance rates at night, as opposed to during the day.
22
23 The rate of disappearance was also higher in the autumn than in the winter (RM
24 ANOVA: $F_{1,192}=13.563$, $P=0.009$). Further investigation of the interactions between

1 time of day and season (Table 1) shows that nocturnal disappearance rates were
2 higher in the autumn than the winter (RM ANOVA: $F_{1,96}=31.220$, $P=0.001$) (autumn
3 average rate of 1.76% versus winter average rate of 0.44%) whereas there was no
4 seasonal effect in diurnal rates (RM ANOVA: $F_{1,96}=2.960$, $P=0.136$) (autumn average
5 rate of 0.40% versus winter average rate of 0.66%). Due to the interactions with
6 season, a separate analysis of each season was conducted.

7
8 There were no effects of any variables (distribution, day or time of day) or
9 interactions between any variables with respect to rate of disappearance in the winter.
10 This was probably because very few seeds disappeared in winter; by the end of day 3,
11 an average of 18 seeds had disappeared in the autumn whereas only an average of 8
12 seeds disappeared in the winter. In the autumn, there was no main effect of
13 distribution (RM ANOVA: $F_{3,96}=0.832$, $P=0.509$) but there were lower disappearance
14 rates during the day than during the night (RM ANOVA: $F_{1,96}=30.482$, $P=0.012$) (see
15 above average rates) and also lower disappearance rates in later days (RM ANOVA:
16 $F_{2,96}=6.567$, $P=0.031$) (Fig. 3a). There was also an interaction between distribution
17 and time of day (RM ANOVA: $F_{3,96}=5.726$, $P=0.018$). The average disappearance
18 rates for the most hyper-dispersed distribution were 0.99% during the day versus
19 1.34% at night, while the most clustered distribution had a diurnal rate of 0% and a
20 nocturnal rate of 2.25%. A post-hoc analysis of each distribution separately indicates
21 that the disappearance rates were higher during the night than during the day for the
22 Random (Low) (RM ANOVA: $F_{1,24}=11.969$, $P=0.041$), Random (High) (RM
23 ANOVA: $F_{1,24}=8.231$, $P=0.019$) and Clustered distributions (RM ANOVA:
24 $F_{1,24}=1372.232$, $P<0.001$), but not for the Uniform distribution (RM ANOVA:

1 $F_{1,24}=1.026, P=0.286$) (Fig. 3b). To summarize, disappearance rates in the autumn
2 were higher in the night than in the day for all but the uniform distribution.

3

4 **Change in distribution over time (for autumn data)**

5

6 This analysis was only conducted for autumn data because of the low rates of
7 cache loss in the winter. The data were significantly different from normal
8 (Kolmogorov-Smirnov: $Z_{112}=2.677, P<0.001$). A log transformation was used because
9 it made the data less different from normal (Kolmogorov-Smirnov: $Z_{112}=1.432,$
10 $P=0.033$). As expected, the initially more clustered distributions had a higher Index of
11 Dispersion (ID) than the more hyper-dispersed ones (RM ANOVA: $F_{3,112}=48.623,$
12 $P<0.001$; Fig. 4). There was no overall effect of time (RM ANOVA: $F_{6,112}=1.096,$
13 $P=0.402$) but there was an interaction between time and initial distribution (RM
14 ANOVA: $F_{18,112}=7.012, P<0.001$). Considering the initial distributions separately, the
15 ID of the Uniform distribution did not change over time (RM ANOVA: $F_{6,28}=0.734,$
16 $P=0.629$), while the ID decreased with time for the Random (High) (RM ANOVA:
17 $F_{6,28}=7.871, P<0.001$) and Clustered (RM ANOVA: $F_{6,28}=10.764, P<0.001$)
18 distributions. ID increased with time for the Random (Low) distribution (RM
19 ANOVA: $F_{6,28}=4.947, P=0.004$). This indicates that the Random (High) and Clustered
20 distributions became more hyper-dispersed but the Random (Low) became more
21 clustered as time progressed.

22

23

DISCUSSION

This study has provided three interesting results. Firstly, hyper-dispersed distributions reduce cache loss. This is mainly due to higher disappearance rates in the more clustered distributions during the night period, as opposed to the daytime. The reduced cache loss in hyper-dispersed distributions is consistent with other studies that have considered the effect of food distribution on the foraging of fish (Ivlev, 1961; Emlen, 1973), coal tits and great tits (Male & Smulders, in preparation), cattle (Laca, 1998) and ants and rodents (Reichman & Oberstein, 1977; Reichman, 1979). This result is also in agreement with studies which showed that cache loss was density dependent (Stapanian & Smith 1978; Sherry et al. 1982; Stapanian & Smith 1984; Waite 1988) because, in essence, distribution is a manipulation of local density. Therefore, hyper-dispersed distributions increase the survival of food items when exposed to a range of foragers. Our second finding is that the most clustered distributions of seeds became more hyper-dispersed as time progressed. This is consistent with our first finding as the clustered areas of these distributions were removed most rapidly by foragers, presumably using local area searches. Finally, we found that fewer seeds disappeared during the winter than during the autumn.

This last finding seems counterintuitive (but consistent with Brodin (1993)), as it was expected that in the winter, all animals would require more food so foraging would increase and the number of seeds remaining would decrease. There are a number of possible explanations for this finding: firstly, snow cover, which may increase the difficulty of foraging, was present during winter. This might explain the results, but only partly, as snow was only present for two out of the four winter trials.

1 Secondly, a lack of olfactory cues in the winter due to the freezing of food, which
2 reduces the release of odorant molecules (Vander Wall 1998), may be a contributing
3 factor, especially if the major foragers rely on olfactory cues (e.g. rodents as in Sherry
4 et al.'s (1982) and Tomback's (1980) studies). Finally our results may be due to a
5 reduction in the number of foraging animals in the winter because of hibernation,
6 migration and the general decrease in population numbers due to higher mortality
7 rates than birth rates at this time of year. We hypothesize that the population decrease
8 of foragers is probably the most influential, as there are numerous small rodents found
9 within the Reserve (such as bank vole (*Clethrionomys glareolus*), field vole (*Microtus*
10 *agrestis*), water vole (*Arvicola terrestris*) and the woodmouse (*Apodemus sylvaticus*)
11 (Hammock & Noble-Rollin 1990)), all of which would be expected to decrease in
12 population in the winter. Higher disappearance rates at night (see below) and in the
13 autumn implicate these nocturnal mammals, which have high population numbers in
14 the autumn, as important foragers in our study.

15

16 Our low disappearance rates in the winter appear to be intermediate between
17 Brodin's (1993) results with Scandinavian willow tits and the high rates reported by
18 Sherry et al. (1982) in Wytham Woods near Oxford. This may be due to differences in
19 experimental techniques as we used an area with foraging mixed tit flocks and
20 generated artificial caches; Sherry et al. (1982) used marsh tit territories where the
21 birds frequently hoarded and recovered sunflower seeds and also generated artificial
22 caches; and Brodin (1993) re-baited real willow tit caches that had been emptied.
23 Alternatively, there may be differences in these habitats (Scandinavian coniferous
24 forest, mixed deciduous/coniferous woodland in the north of England and mainly
25 deciduous woodland in the south of England), such as differences in the numbers or

1 types of seed eaters which create differences in pilfering rates. Although attempts
2 were made to imitate marsh tits' hoarding locations, it is possible that the artificial
3 caches had higher loss rates in general than the actual caches made by the parids in
4 Brodin's (1993) study due to the experimenter's poor hoarding technique.

5
6 Our data also provide some information about the foraging strategies used by
7 animals at different times of day. Nocturnal foragers tended to forage nearer the
8 ground whereas diurnal foragers appeared to prefer higher sites. Generally,
9 disappearance rates were higher at night (in contrast to Cowie et al. 1981 and Brodin
10 1993), suggesting that there were either more foragers around at night, or they were
11 more efficient in their foraging. It is possible that our disappearance rates at night
12 were higher than other studies because the major foragers in this study may have been
13 nocturnal rodents, whereas in Brodin's (1993) study they may have been mainly
14 diurnal birds. The higher rates occurred especially in the most clustered distributions
15 indicating that nocturnal foragers employed area-restricted search strategies. These
16 findings may of course be specific to the types of cache sites which we created.
17 However, it is known that at least some species of hoarding birds (e.g. marsh tits;
18 Sherry et al. 1982), use similar cache sites close to the ground. We should also make it
19 clear that not all the seeds that disappeared before the morning check necessarily
20 disappeared during the night. Checks were conducted just after sunrise and whilst the
21 first array was being checked for overnight cache loss, the other arrays may have been
22 exposed to foraging by birds because the hours during the morning are one of the peak
23 foraging times for birds (Bednekoff & Houston 1994). This suggests that the recorded
24 nocturnal disappearance rates may be artificially inflated. On the other hand, other
25 evidence indicates that early morning foraging is limited by light intensity (Kacelnik

1 1979) indicating that the nocturnal rates may not be affected by our system of
2 checking caches. Regardless of the effects of these time checks, rodents are still likely
3 to be the major foragers in the study because the seasonal variation in cache loss
4 corresponded with their population numbers and because lower caches were more
5 likely to disappear than higher ones, a pattern not expected from foraging birds.

6

7 **Implications for food hoarding**

8

9 The finding that hoarding animals should aim for a more hyper-dispersed
10 cache distribution may be especially relevant for long-term hoarders. This is because
11 the caches of long-term hoarders are exposed to foragers for longer periods of time
12 which increases the odds of pilferage (Vander Wall & Jenkins 2003). Even though it
13 is unlikely that animals will ever obtain a strictly uniform distribution, our data show
14 that even an approximation of a more hyper-dispersed distribution will be
15 advantageous. There is some evidence that food-hoarding animals may behave in a
16 way to avoid clustering their food. In the lab, marsh tits tended to avoid the storage
17 sites with seeds from a previous hoarding session when hoarding more food in a
18 second hoarding session (Shettleworth & Krebs 1982). In the field, gray jays tended to
19 avoid caching in extant cache-dense areas and dispersed caches made on a second
20 encounter more widely (Waite & Reeves 1992; Waite & Reeves 1994; Waite &
21 Reeves 1995). However, other field studies suggest that some hoarders may generate
22 clustered distributions (Stapanian & Smith 1978; Cowie et al. 1981; Clarkson et al.
23 1986; Barnea & Nottebohm 1995; Hurly & Lourie 1997). This may be because some
24 of these studies did not consider the distribution of the caches themselves, but instead
25 considered the distribution of directions taken when hoarding food from a central food

1 source. This does not give us detailed information about the final distribution
2 generated, especially as hoarders are known to re-cache hoards (Brodin 1994b).
3 Alternatively, clustered distributions may sometimes be generated because there are
4 numerous factors which influence hoarding behaviour and minimizing cache loss is
5 only one of them. The risk of losing access to caches, exposure to predators and
6 energy expenditure during hoarding and retrieval are examples of factors which may
7 also influence the distributions of caches. As such, hoarders may be constrained by
8 other factors when it comes to establishing their cache distributions. For example,
9 individual crested tits cache uniformly within the full 360° around a food resource
10 whereas willow tits cache in certain directions generating a non-uniform distribution
11 (Jokinen & Suhonen 1995). This may be because willow tits are subordinate to
12 crested tits so they may be forced to use suboptimal hoarding locations. Similarly,
13 black-capped chickadees (*Parus atricapillus*), only deviated from the use of hyper-
14 dispersed distributions of caches around forest edge feeders (Brotons et al. 2001)
15 perhaps because these sites are exposed with increased predation risk or because there
16 are a limited number of possible cache sites at forest edges.

17
18 Hyper-dispersing appears to reduce cache loss but it may also reduce cache
19 recovery by the hoarders themselves. Cache distributions may be generated which
20 represent a trade-off between minimizing pilferage and maximizing cache retrieval
21 (Barnea & Nottebohm 1995). On the other hand, hoarders may hyper-disperse caches
22 to reduce loss and then use additional strategies to enhance cache recovery, such as
23 memory-based retrieval (Cowie et al. 1981; Sherry et al. 1981; Sherry 1982;
24 Shettleworth & Krebs 1982; Shettleworth 1983; Sherry 1984a; Sherry 1984b; Brodin
25 & Kunz 1997) and specific hoarding and foraging niches (Haftorn 1956; Pravosudov

1 1986; Alatalo & Carlson 1987; Suhonen & Alatalo 1991; Suhonen & Inki 1992; Inki
2 & Suhonen 1993; Brodin & Kunz 1997). We are currently investigating the respective
3 role of memory and hoarding/foraging site preferences during cache recovery in a lab
4 experiment.

5
6 Many hoarding animals share territories with other hoarders, and one might
7 expect that this would result in overlapping cache distributions and therefore
8 clustering. This should not be a problem because, although overlapping cache
9 distributions increase the likelihood that an individual hoarder's caches are found in
10 the first place, the hyper-dispersing of the cache distribution reduces the probability
11 that all of its caches are pilfered at the same time. In other words, if hyper-dispersed
12 cache distributions are used, the discovery of a cache made by Hoarder 1 may
13 increase the likelihood of finding a cache made by Hoarder 2 but decreases the
14 likelihood of finding another cache made by Hoarder 1. Hyper-dispersing therefore
15 ensures that hoarding is adaptive (Andersson & Krebs 1978) by preventing pilferers
16 from simultaneously discovering a number of caches made by the same hoarder.

17
18 Intriguingly, overlapping hyper-dispersed cache distributions may actually be
19 an advantage to hoarders that employ a cache hyper-dispersing strategy because they
20 appear clustered or, at best, random to the foragers. Foragers are likely to evolve
21 foraging strategies which increase foraging efficiency on the general food distribution.
22 Some foragers (Dall & Cuthill 1997; Dall et al. 1997; Hill et al. 2000; Hill et al. 2002;
23 Hill et al. 2003) are also capable of adapting their foraging strategy to the given food
24 distribution through habitat assessment. Foraging strategies cannot evolve and
25 foragers cannot adapt to enhance foraging efficiency on hyper-dispersed cache

1 distributions if they overlap because they do not appear hyper-dispersed from the
2 perspective of the forager. As these overlapping hyper-dispersed cache distributions
3 have some clustering, a local area search, such as an area-restricted search (Tinbergen
4 et al. 1967), should increase foraging efficiency both in the autumn, when the
5 available food mainly consists of clustered seed, nuts and insects, and in the winter,
6 when the available food mainly consists of over-lapping hyper-dispersed cache
7 distributions.

8
9 Assuming that some hoarders do aim to hyper-disperse their caches
10 (Shettleworth & Krebs 1982; Waite & Reeves 1994), the next question is how these
11 distributions are generated? A role for spatial memory in the placement of scattered
12 caches has been suggested previously (Waite & Reeves 1994; Smulders et al. 1995;
13 Smulders & Dhondt 1997; Smulders 1998; Smulders et al. 2000) but this idea has
14 always been controversial. We are actively investigating this idea. However, even if
15 birds do not adopt a hyper-dispersing strategy per se, our results show that there are
16 other aspects of the natural world that promote the survival of long-term scatter
17 hoards. Firstly, total cache loss is lower in the winter than in the autumn. If this is
18 indeed due to dwindling populations of foragers, it should apply not only in the
19 understory, but everywhere in the forest. Secondly, cache distributions tended to
20 converge on fairly dispersed distributions over time, as a consequence of cache loss.
21 This means that more clustered distributions over time will become more hyper-
22 dispersed as the clustered sections are removed by foragers using local area searches.
23 Therefore, a hyper-dispersed distribution may be generated if a hoarding animal
24 simply stores many food items randomly and allows cache loss to gradually produce a
25 more hyper-dispersed distribution. Theoretically, provided a hoarder generates a large

1 enough number of caches, clustered sections would be removed by some exposure to
2 foragers and the resulting hyper-dispersed distribution would reduce long-term loss of
3 the remaining caches. The question then becomes whether it is more economical (i.e.
4 evolutionarily adaptive) to invest in hoarding more items, or to invest in a hyper-
5 dispersing strategy. There are costs to both strategies; the time and energy spent
6 hoarding the food which is lost to pilferers is the cost of hoarding food randomly and
7 the enhanced memory that would be required to remember the locations of previously
8 hoarded items is the cost of hyper-dispersing caches. There is evidence that some tit
9 species hoard very large numbers of food items (up to 170,000 items in one autumn)
10 (Haftorn 1959; Pravosudov 1985). We are currently investigating the conditions under
11 which either strategy would be adaptive.

12

13 **Conclusion**

14

15 This study suggests that hyper-dispersed distributions reduce seed loss
16 indicating that adopting a hyper-dispersing strategy would be adaptive to hoarding
17 animals. Over time, more clustered distributions converge on more hyper-dispersed
18 patterns, improving the survival probabilities of the remaining items. Once autumn is
19 past and winter starts, survival rates also increase. All of this acts in favour of long-
20 term cache use.

21

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2
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9
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8

1

Table 1: RM ANOVA results for the Rate of Disappearance

2

Variables	df	n	F	P
Distribution	3	192	0.382	0.767
Day	2	192	0.354	0.070
Time of Day	1	192	16.792	0.006
Season	1	192	14.365	0.009
Distribution x Season	3	192	0.285	0.836
Day x Season	2	192	3.923	0.049
Time of Day x Season	1	192	31.886	0.001
Distribution x Time of Day	3	192	3.385	0.041
Distribution x Day	6	192	0.903	0.503
Day x Time of Day	2	192	1.117	0.359
Distribution x Day x Season	6	192	61.364	0.256
Day x Time of Day x Season	2	192	3.998	0.047
Distribution x Time of Day x Season	3	192	2.151	0.129
Distribution x Day x Time of Day	6	192	1.814	0.124
Distribution x Day x Time of Day x Season	6	192	0.489	0.812

3

4

1 **Fig. 1:** The four different seed distributions used in this study. Axes represent
2 distances in metres.

3

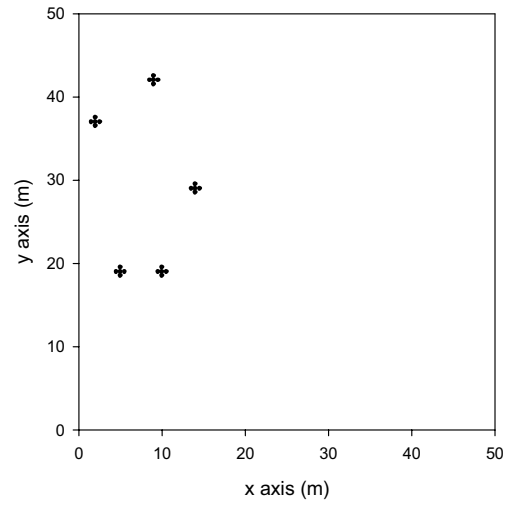
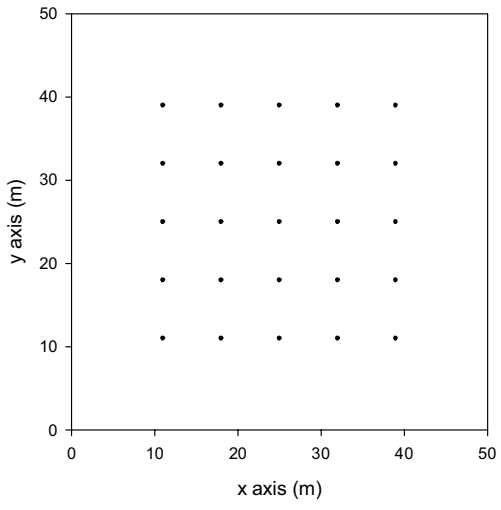
4 **Fig. 2:** Average numbers of seeds remaining for each distribution over time.
5 Significantly more seeds remained in the Uniform than in the Random (High) and the
6 Clustered Distributions, and in the Random (Low) than in the Clustered Distribution.
7 We plotted the means across all trials, excluding error bars because the analyses were
8 done as a repeated-measures GLM, thus controlling for across-trial variability. Lines
9 were fitted as exponential decay curves for each distribution.

10

11 **Fig. 3:** The mean percentage of seeds that disappeared per hour for each distribution
12 (autumn data only) (a) plotted against time and (b) plotted by distribution. Note the
13 higher disappearance rates of seeds at night in all but the uniform distribution. Error
14 bars in (b) indicate 95% confidence intervals.

15

16 **Fig. 4:** Changes in the average Index of Dispersion ('ID') over time for all
17 distributions (autumn data only). Distributions that start out clustered (high ID) or
18 hyper-dispersed (low ID) become more hyper-dispersed (low ID) or more clustered
19 (high ID) over time respectively. Lines were fitted by least square regression. The
20 large difference in the ID of the initial distributions make changes over time difficult
21 to read so Log Average ID is plotted on the y axis.

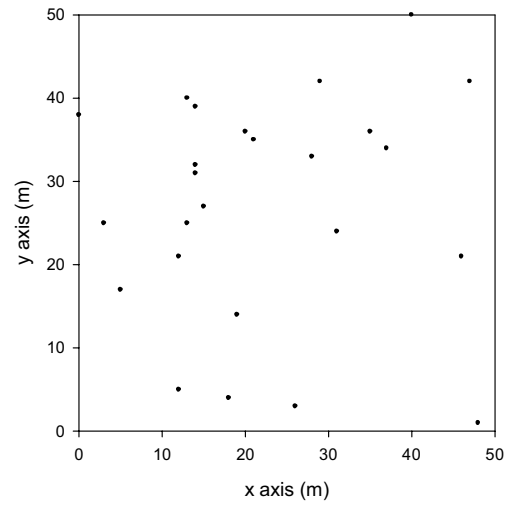
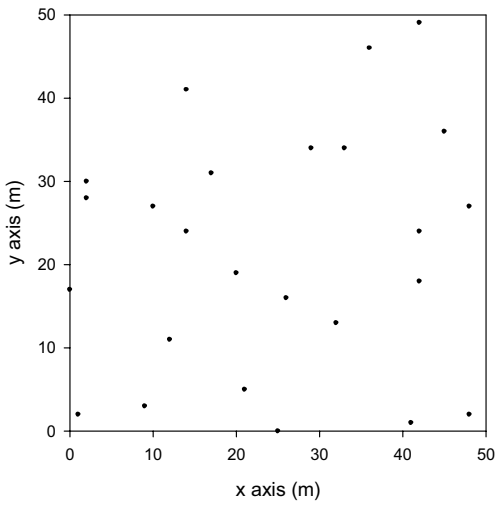


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(a) Uniform

(b) Clustered



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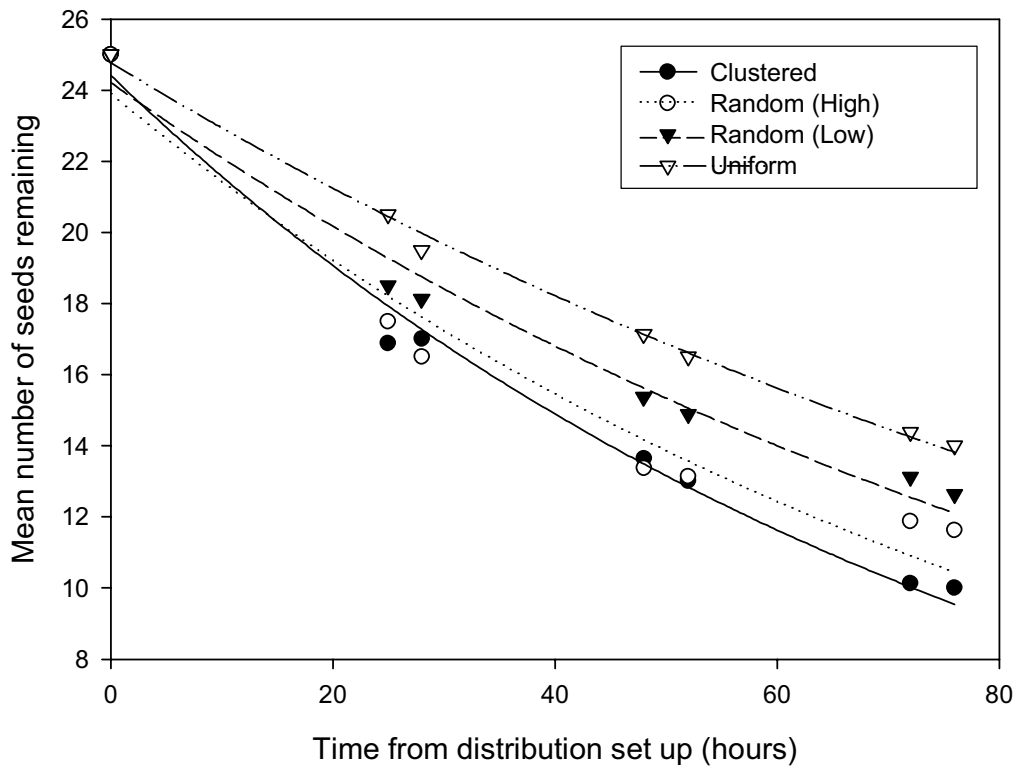
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(c) Random (Low)

(d) Random (High)

5

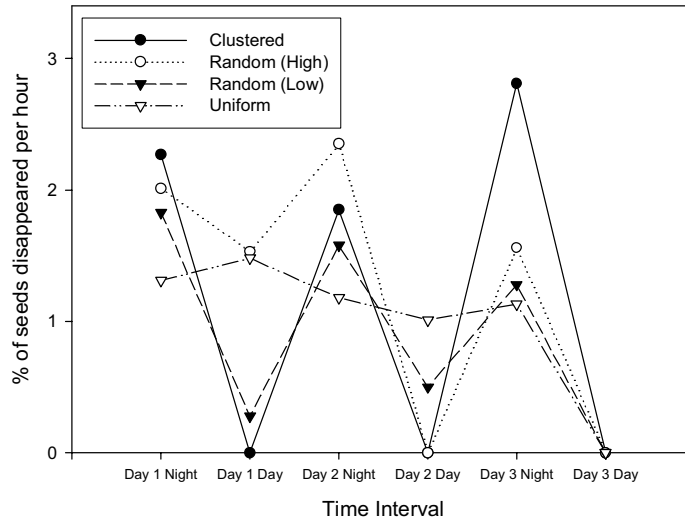
Fig. 1



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Fig. 2

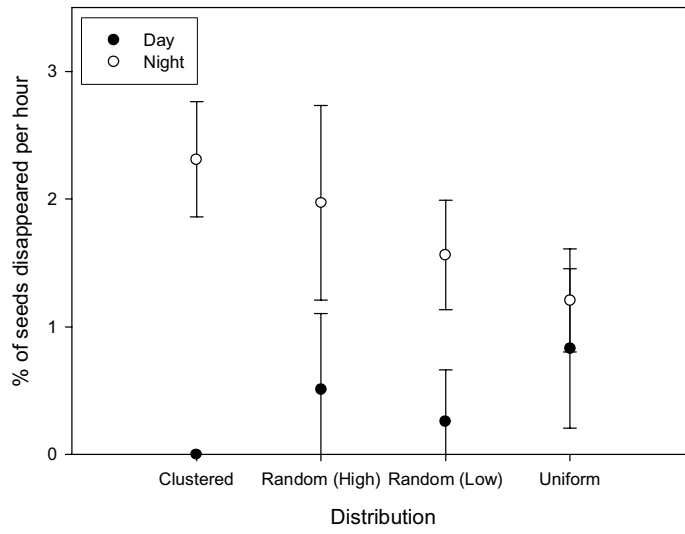
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(a)



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Fig. 3

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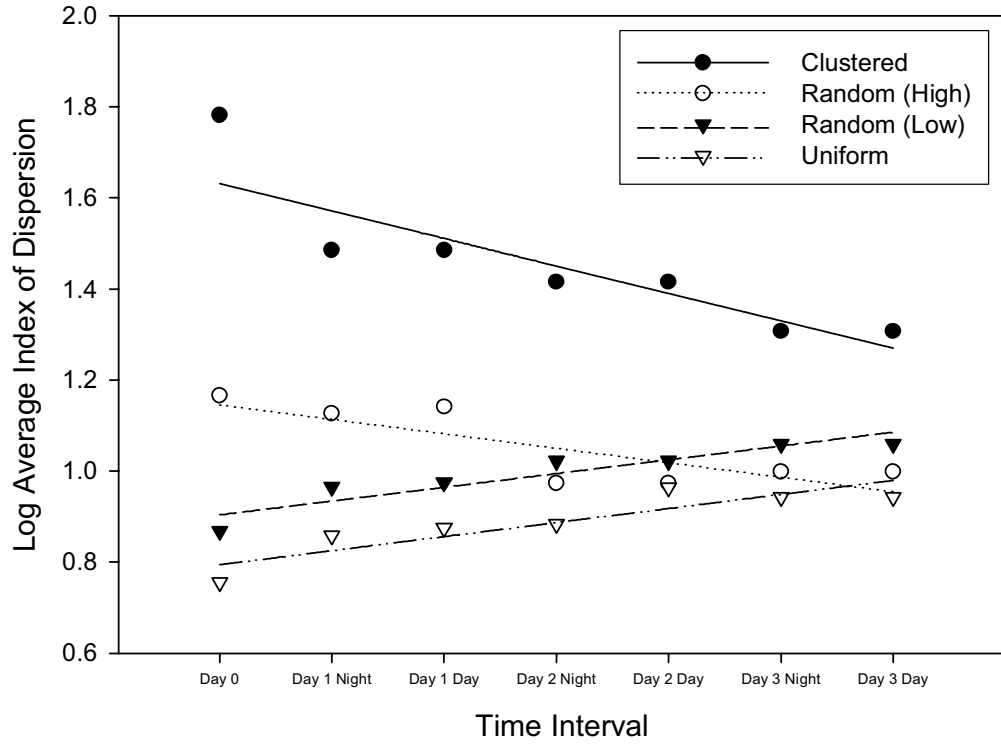


Fig. 4