JOURNAL OF THE ROYAL SOCIETY Interface

J. R. Soc. Interface (2012) **9**, 869–879
doi:10.1098/rsif.2011.0581

A search game model of the scatter hoarder's problem

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Scatter hoarders are animals (e.g. squirrels) who cache food (nuts) over a number of sites for later collection. A certain minimum amount of food must be recovered, possibly after pilfering by another animal, in order to survive the winter. An optimal caching strategy is one that maximizes the survival probability, given worst case behaviour of the pilferer. We modify certain 'accumulation games' studied by Kikuta & Ruckle (2000 *J. Optim. Theory Appl.*) and Kikuta & Ruckle (2001 *Naval Res. Logist.*), which modelled the problem of optimal diversification of resources against catastrophic loss, to include the depth at which the food is hidden at each caching site. Optimal caching strategies can then be determined as equilibria in a new 'caching game'. We show how the distribution of food over sites and the site-depths of the optimal caching varies with the animal's survival requirements and the amount of pilfering. We show that in some cases, 'decoy nuts' are required to be placed above other nuts that are buried further down at the same site. Methods from the field of search games are used. Some empirically observed behaviour can be shown to be optimal in our model.

Keywords: scatter hoarder; food caching; resource diversification; search game

1. INTRODUCTION

Animals require a minimum consumption of energy over time in order to survive, where the minimum level may depend on random variables such as activity or ambient temperature. To achieve this consumption when internal storage of energy (e.g. fat or other chemical processes) is not available, some animals are forced to cache food during the foraging season to recover it later, in the winter or a dry season. Some of these animals, known as *scatter hoarders*, disperse their food supply over several locations and dig to various depths to deposit them.

A problem with external caching of food is that in the period between caching and retrieval, some of it may be lost, either through natural events such as floods, or through pilfering by other animals. So in order to maximize the probability of surviving the winter, the total problem faced by the scatter hoarder has at least the following elements of optimization:

(i) how much effort to spend on foraging (food accumulation);
(ii) how much effort to spend on caching (e.g. total digging);
(iii) how to choose the number of caches;
(iv) how to determine the sizes of the caches; and
(v) how to distribute the food vertically at each site (caching depth).

A full production-inventory model that includes all these elements is beyond the scope of this paper. Also, the possibility that cachers may also be pilferers is beyond the scope of our game theoretic model, so we must assume that these are distinct. Our main model, based on ideas from the field of search games, assumes that the first three parameters (i)–(iii) are given. That is, we take the perspective of say a squirrel who has m nuts to hide (i), can dig to a total depth of D_S (ii), and can hide the nuts over n sites (iii). If we take our unit of digging length to be D_S, we can normalize this to $D_S = 1$; so we are left with two squirrel parameters m and n. The squirrel's problem is how to place the m nuts at the n sites (potential digging locations), subject to the restriction that the sum of the depths of the holes is no more than 1 (that is, the caching effort $D_S = 1$). The two parameters m and n determine the squirrel's feasible caching strategies, but to determine which strategies are good, the squirrel needs to know two more parameters. Firstly, he needs to know the minimum number k of nuts that must be available at retrieval time in order to survive the winter. Secondly, he needs to know the total digging depth $D = D_P$ that a pilferer has (or pilferers have) available. The number D can be thought of as an indirect

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Received 28 August 2011
Accepted 27 September 2011

measure of the amount of loss he can expect between caching and retrieval. In theory, he might only know the *distribution* of D (a harder problem we will only touch on here). The four parameters m, n, k, D determine what is known as a (zero-sum) *game against Nature* or *maximin problem* $\Gamma = \Gamma(m, n, k, D)$, which we call the *caching game*. It can be described simply as follows.

- The squirrel hides the m nuts at chosen depths at the n sites.
- The pilferer digs at the various sites to a total depth of D, removing any nuts he finds.
- The squirrel *wins* (payoff is 1) if there are at least k nuts left (otherwise, he loses; payoff is 0).

The well-known theory of zero-sum games says that this game has a value, which we call P, or $P(D)$ to show dependence on D, which represents in this case the maximum probability of surviving the winter that the squirrel can guarantee against any digging strategy of the pilferer.

The main theoretical contribution of the paper is the solution of the caching game Γ for some parameters. This means in particular that we find the randomized dispersal and depth strategy for the squirrel, which maximizes the probability of surviving the winter (having k nuts left), against a worst case pilfering strategy. Our view (as is usual in games against Nature) is asymmetric; we view the squirrel as an actual agent, but view the pilferer as a theoretical worst case of Nature. In this sense, we determine optimal caching strategies of scatter hoarders, but not strategies that we would recommend to pilfering animals (who might well have other objectives than defeating squirrels). Our model is very abstract and very general—our analysis is too simple at the moment to be applicable to the study of particular species. However, we believe that this approach gives an insight into the scatter hoarder's problems and with further development may indeed help in the understanding of particular caching and pilfering behaviours.

The model we present here is new and belongs to the field of search games as studied in Garnaev [1] and Alpern & Gal [2]; and more generally that of geometric games [3]. More particularly, it is related to games called *accumulation games*, as developed earlier [4–8]. These are somewhat more complicated than caching games in that the hider (squirrel, in our formulation) repeatedly adds material (corresponding to our nuts) to the hiding sites, as they are pilfered over time. On the other hand, the depth of caching is not modelled. These games were aimed at military or economic applications, where the stored material could be armaments or perhaps financial investments in companies that might collapse (equivalent to loss of nuts through storms or pilfering). The Kikuta–Ruckle theory has recently been studied by applying combinatorial ideas [9–11]. However, this article represents the first attempt to model the problem of *depth of caching* at a site.

2. RELATION TO THE SCATTER-HOARDING LITERATURE

The nature of dispersal and digging strategies adopted by various species of scatter hoarders has been widely studied in the field and laboratory. This literature has raised a number of theoretical questions for which our model may be relevant. However, this section also discusses issues that are not modelled in our caching game, but could indeed be modelled in more elaborate versions of our game.

Indeed, the caching or hiding of food items for later consumption is widespread among birds and mammals [12], and different species may use different tactics shaped by the different ecological challenges that they face [13]. Food-caching corvids—birds in the crow family that includes the ravens, magpies and jays—for example, cache perishable foods such as worms as well as non-perishable nuts, and these birds can remember not only where they cached the various food items, but also how long ago, thus enabling them to recover the perishable foods before they have become degraded and inedible (see Clayton & Dickinson [14] and Zinkivskay *et al.* [15], reviewed in Grodzinski & Clayton [16]). By contrast, squirrels solve the problem of perishability in a different way, by only caching the non-perishable nuts [17].

Caching is risky, however, because other individuals may attempt to steal as many of those items as they can. Cache-pilferage is a great problem for storers, with pilferage proportions ranging between 2 and 30 per cent per day, at least for artificial caches [18]). If the pilferage rate is high enough for the average non-cacher to do better than the average cacher, then caching behaviour may be selected against [19] unless there is reciprocal pilferage in which each cacher not only hides their own food, but also steals that which others hide (see Smulders [20] and Vander Wall & Jenkins [18]). It is argued in Andersson & Krebs [19] that for caching behaviour to be maintained as an evolutionarily stable strategy, the cacher should rely on spatial memory and other mechanisms that enhance successful and efficient cache recovery by the original hoarder, thereby giving them a recovery advantage over potential pilferers [21]. However, in addition to spatial memory, cachers have evolved a variety of cache-protection strategies to reduce the pilferage risk [22]. For example, they use distance, shade and barriers to minimize the chance that onlookers can accurately see where the cacher has actually hidden the food. Indeed, it has been suggested that this is why many species scatter hoard their food caches in multiple locations rather than merely defending a single larder [12]. Hiding food items in many (dispersed) locations reduces the probability that the bulk of their caches will be found by the other animals foraging in the same area [23–28]. What is less clear, however, is how the scatter hoarder should best optimize the distribution of such scattered caches, i.e. how many locations should be used, and how many items should be cached in each location. A further question concerns cache depth: should individuals vary the depth at which they hide their caches and, if so, what is the optimal way to do so? There is also a trade off between digging deeper so that the cache is buried at a greater depth and the likelihood of being spotted in the act of caching by would-be thieves.

For many species including some tits and chickadees, it is thought that the pilferers, or cache-robbers, come across the caches by chance. Some mammals such as squirrels may use smell, at least in part, to find the caches of others [12]. But for birds that have a poor sense of smell, a more accurate method is to rely on memory of where the individual has cached [21]. Furthermore, the ability to locate caches made by others quickly and efficiently may be the important difference between successful cache-robbing and potential aggression from the individual that hid the food. So an obvious advantage of observing and remembering where others have cached is that it allows a thief with observational memory to efficiently steal caches when others have left the scene, thereby eliminating both the costs of caching and of fighting. Corvids that are renowned for their intelligence [29] do rely on observational memory when stealing the caches that other birds have made (see Dally *et al.* [22] for a comprehensive review).

There is certainly good evidence to suggest that cachers are sensitive to whether or not other individuals are present at the time of caching and that they can use protective tactics to minimize the risk of cache loss. Here, too, the details vary from species to species. A simple strategy is employed by the Merriam's kangaroo rat, for example: this solitary species usually scatters many caches throughout its territory, but if it sees another rat stealing its caches then it switches from scattering lots of caches to defending a single larder [30]. In squirrels, it was found in Leaver *et al.* [31] that grey squirrels not only space their caches further apart, but also with their back to potential thieves thereby blocking the onlooker's view, but they do so only if the onlookers are fellow grey squirrels. Interestingly, this is not the case if the thief is a heterospecific corvid, suggesting that the squirrel's sensitivity to the risk of cache loss is somewhat limited. One reason for this may the evidence of Hopewell *et al.* [32, p. 1143] that

> ... scatter hoarders respond to conspecifics at a food source primarily as competitors rather than as potential pilferers; the squirrels increased the rate at which they returned to the nut patch when conspecifics were present rather than transport the nuts farther away to minimize the risk of pilferage. In contrast, and in line with previous studies, the squirrels responded to a reduction in the availability of food by increasing the distance at which they stored the food from the source.

In the case of corvids, however, the cache protection tactics are even more developed, perhaps because of the cognitive challenges and demands imposed by the fact that the pilferers rely on observational memory to steal the caches whenever they wish so [33]. These birds not only adjust their caching behaviour in the presence of a conspecific audience [34–37], but they also keep track of which particular individual was watching when they cached and take protective action accordingly, moving those caches that particular bird has watched them cache [38]. Furthermore, some species even attend to heterospecific observers as well as conspecific ones, differentiating between the risks that conspecifics and heterospecifics represent to their caches. Stellar's jays steal grey jays' caches, whereas both grey jays and Clark's nutcrackers do not steal. Thus, while grey jays cache as usual in front of a conspecific or a Clark's nutcracker, they cease caching in the presence of a Stellar's jay [39].

Corvids also differentiate between knowledgeable and ignorant potential pilferers, adjusting their caching tactics accordingly [40] and young ravens, in developing their skills, use play caching to assess this [41]. Furthermore, they make use of a variety of 'deceptive' strategies, which function to reduce the risk of disclosing information about the location of their own caches, by hiding the food behind barriers so that the potential pilferer cannot see, and using distance and shade to reduce the visual acuity of the onlookers [34,35,42,43], and even know when to conceal auditory information, namely when the potential pilferers can hear but cannot see [44]. But perhaps most striking of all is the fact that these cache protection tactics depend on having had the specific experience of being a thief oneself. Ignorant corvids who have not pilfered any caches do not engage in these behaviours [36]. This finding suggests that these thieves relate information about their previous experience as a cache-robber to the possibility of future stealing by another individual, and change their caching strategy accordingly, suggesting that 'it takes a thief to know a thief'.

Scatter hoarding appears to reduce the proportion of caches that are lost, as a number of studies have found that widely spaced caches are more likely to survive than caches placed close to one another [30,45–47]. There is also evidence, albeit limited, to suggest that storers adjust the density at which they cache as a function of their social status. For example, territorial (breeding) common magpies make their caches closer together, and nearer to the food source, than non-breeders [48]. This difference in cache spacing is thought to occur because magpie caches are most often stolen by conspecifics. Thus, birds with exclusive territory use would experience less cache pilferage, a factor that would be reflected in their 'optimal' cache density [49]. While the ecology of territorial and non-breeding magpies might differ significantly, and therefore have implications for their use of cache sites, this finding highlights the need for further research on the sensitivity of food-storers to the risk of cache theft.

3. THE GAME Γ

We assume the squirrel has m nuts and needs k of them to survive the winter ('win'); so he wishes to hide them in such a way as to maximize the probability that k nuts remain after pilfering. This assumption is based on the observation that if fewer than k nuts remain, the actual number only affects how long into the winter the squirrel will survive, and thus does not greatly affect his fitness (which is very low in any case). If more than k nuts remain, the actual number does affect fitness somewhat. But it seems that our binary cutoff criterion of k nuts does capture the essential problem. To complete the squirrel's side of our model, we assume that there are n potential caching sites. A 'site' represents a location where a single hole might be dug, and where one or more nuts might be placed at different depths. We assume that the squirrel has enough energy to dig a total depth D_S (S for squirrel) at these sites. That is, the sum of the depths reached at all the sites cannot exceed his energy resources D_S. Thus, a squirrel strategy describes how he places his m nuts at various depths among the n caching sites, subject to his energy (digging) constraint D_S. He has the option of placing nuts at different depths at the same site, although this may not at first glance appear to be a good idea.

After the squirrel places his nuts, the pilferer arrives. He knows the location of the n sites but not which ones have nuts or at what depths they are hidden. He can dig to different depths at the sites, subject to his own energy constraint that the total depth (summed over all sites) does not exceed some constant D_P (P for pilferer). A *smart* pilferer can make future digging plans that depend on what he has found so far; a *normal* pilferer can just choose the depths at each site. In this note, we will analyse both cases. An empirical question raised by this distinction is whether pilferers switch sites when they find a cache (one or more nuts placed at a certain depth at a site), or continue to look for a deeper cache at the same site. We assume throughout that the pilferer can only detect a nut visually, when the earth above it has been removed. No other signals (e.g. olfactory) are available.

3.1. Optimal strategies with smart pilferers, $m = n = 2$, $k = 1$

To illustrate the ideas involved in calculating $P(D)$, we analyse the simple case where the squirrel has to hide two nuts at two sites and survives (wins) if at least one nut remains after pilfering (the parameter values are $m = n = 2$ and $k = 1$). We note that the theory of zero-sum games requires that, in general, the squirrel will have to use randomized strategies (called *mixed strategies*) in order to achieve the best survival probability $P(D)$. Here, we assume the pilferer is smart, as defined already, in that he can alter his digging depending on what he does or does not find up to a given time.

We assume, without loss of generality, that the squirrel can dig to a total depth $D_S = 1$, and he needs one nut left after pilfering to survive and hence 'win' the game. We also assume the pilferer has a fixed total depth $D_P = D$ to which he can dig, which may be a sum of depths dug in each hole. We no longer need the subscript on D to distinguish the pilferer's digging from the squirrel's, as the squirrel's has been normalized to 1. So

$$D = \frac{D_P}{D_S}.$$

Note that if $D < 1$, the squirrel can always win ($P(D) = 1$) by hiding both nuts together in one site at depth 1. If $D \geq 2$, and the pilferer digs to depth 1 at each of the two separate sites, any nuts placed by the squirrel will be lost. Thus, there cannot be any strategy for the squirrel giving him a positive probability of surviving, and hence in this case $P(D)$ is 0. To exclude these trivial cases, we assume that $1 \leq D < 2$. The solution of this problem splits into two cases:

Proposition 3.1. *If the pilferer's digging depth constraint D satisfies $3/2 \leq D < 2$, then it is optimal for the squirrel to place both nuts at maximum depth 1 at a single random site. In this case, the maximin survival probability $P(D)$ is $1/2$.*

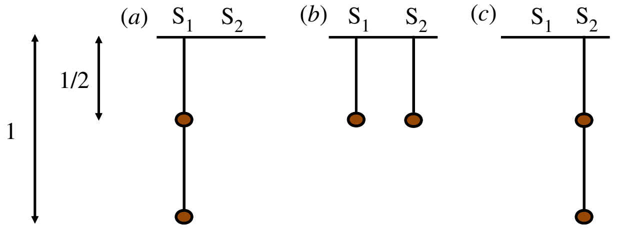

Figure 1. Three caching strategies of the squirrel. (Online version in colour.)

Proof. Suppose the squirrel places both nuts at depth 1 at a site chosen randomly. Then because $D < 2$, the pilferer cannot dig to depth 1 at both sites, and if he guesses wrongly (which has probability 1/2) he will dig at the wrong site and the squirrel will survive. This squirrel strategy thus guarantees a survival probability of 1/2. There may be a better squirrel strategy, but certainly this shows that $P(D) \geq 1/2$.

The pilferer can guarantee the squirrel will win with probability no more than 1/2 by digging to depth 1 at one site and to depth 1/2 at the other (choosing equiprobably between the sites). It is then easy to verify that however the nuts are buried, the pilferer will find them both at least 1/2 the time. To see this, note that the squirrel can plant a nut at a depth greater than 1/2 at only one site, and if this is the site where the pilferer digs to depth 1, the squirrel loses. Because this occurs with probability 1/2, we have established the claim that $P(D) \geq 1/2$.

Combining the bounds on $P(D)$ demonstrated in the previous two paragraphs shows that $P(D) = 1/2$, as claimed in the proposition. ■

Proposition 3.2. *If the pilferer's digging depth constraint D satisfies $1 \leq D < 3/2$, then it is optimal for the squirrel to hide his two nuts at depths 1/2 and 1 at a single random site, with probability 2/3; and at depth 1/2 at each of the two sites, with probability 1/3. (The three equiprobable configurations are shown in figure 1, where S_1 and S_2 denote the two sites.) In this case, his maximin survival probability $P(D)$ is 2/3.*

Proof. Suppose that the squirrel hides his two nuts at depths 1/2 or 1 in one of the configurations shown in figure 1, with equal probabilities of 1/3 for each. It is easy to see that the pilferer's digging constraint $D < 3/2$ prevents him from finding both nuts in more than one of these three hiding configurations: if the pilferer digs to depth 1 at one site, he will win in one of the configurations (a) or (c) but in neither of the others; otherwise, he will only be able to win in configuration (b). Consequently, $P(D) \geq 2/3$.

Suppose that the pilferer adopts the following two digging strategies with probability 2/3 for *stay* and 1/3 for *switch*: (*stay*) pick a random site and dig to the bottom; (*switch*) dig at a random site and switch to the other site if and when you find a nut. Now any strategy of the squirrel can be characterized as either a *one-site strategy* (both nuts at the same site) or a

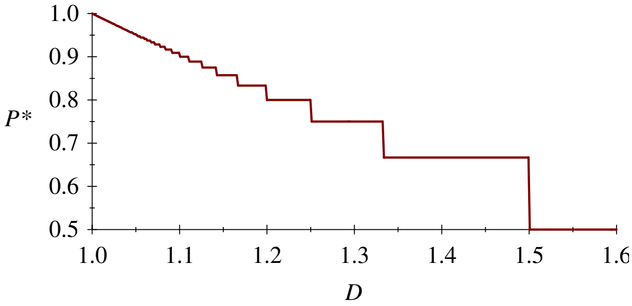

Figure 2. Survival probability $P^*(D)$ against normal pilferers, $1 \le D \le 2$. (Online version in colour.)

two-site strategy (one nut at each site). If the squirrel adopts a one-site strategy, he will *lose* half the time against *stay* and so will lose the game with probability at least $(1/2)\cdot(2/3) = 1/3$. Similarly if he adopts a two-site strategy, he will lose against *switch* (regardless of his two depths, because they sum to only 1), so with probability at least 1/3. So in any case, he loses with probability at least 1/3, and hence $P(D) \le 2/3$.

Combining the two bounds on $P(D)$, we have $P(D) = 2/3$. ■

The strategy drawn in figure 1 for the squirrel has the unusual property of nuts at different levels at the same site. Why can the squirrel not improve (or at least do as well) by changing the placement in cases (a) and (c) to putting both nuts at the bottom? To see why this does not work, suppose that the pilferer always uses the switch strategy. Then the squirrel loses *always* when he adopts (b) and loses half the time when he adopts (a) or (c). So if, as before, he adopts all three with probability 1/3, he wins (survives) with probability only $(1/2)\cdot(2/3) = 1/3$ which is worse than 2/3.

3.2. Solution for normal pilferers

Note that in the last proof, the pilferer's *switch* strategy requires that he is *smart*, in the sense we defined in §1. Suppose, on the other hand, that the pilferer is *normal*, and adopts a *simple strategy* that picks two depths d_1 and $d_2 = D - d_1$ for the sites, which will be dug without reference to what is found. It is clear that in this version, every squirrel strategy is dominated by one that places the nuts at the two sites with respective depths s_1 and $s_2 = 1 - s_1$. (There is no point in placing nuts at different depths at the same site.) We denote by $P^*(D)$ the squirrel's maximum survival probability against a normal pilferer. Note that we always have $P^*(D) \ge P(D)$.

We now show that restricting the pilferer to simple strategies does not help the squirrel when $D \ge 4/3$, but it does indeed help him when $D < 4/3$. For example, $P(5/4) = 2/3$ but $P^*(5/4) = 3/4$, as given by the later result.

Proposition 3.3. *Let q be a positive integer and let the pilferer's total digging depth D satisfy $1 + 1/(q+1) \le D < 1 + 1/q$. Assume the pilferer is normal, as defined already. Then the optimal squirrel strategy is to pick i randomly from the $q+1$ values 0, 1, …, q and to bury his two nuts at respective depths i/q and $(q-i)/q$ at the two sites, in a random order. In this way, the squirrel achieves the maximin survival probability $P^*(D)$ of $1 - 1/(q+1)$, as shown in figure 2.*

Proof. Consider the squirrel mixed strategy S^q, which picks $s_1 = i/q$ with the $q+1$ values $i = 0, \ldots, q$ taken equiprobably. Suppose a pilferer strategy $d = (d_1, d_2)$ wins against more than one of the squirrel strategies. Then it is clear that it wins against two consecutive ones, say i and $i+1$. Then we must have

$$d_1 \ge \frac{i+1}{q} \quad \text{and} \quad d_2 \ge \frac{q-i}{q};$$

so $D = d_1 + d_2 \ge 1 + \dfrac{1}{q}$,

which is larger than we are allowing. So all but one of the strategies i must win, and hence $P^*(D) \ge q/(q+1)$.

Next consider the pilferer simple mixed strategy of $d_1 = j/(q+1)$ with $j = 1, 2, \ldots, q+1$ chosen equiprobably among the $q+1$ possibilities. If a squirrel strategy s_1 wins against all of these, then for every j we have either

$$s_1 > \frac{j}{q+1} \quad \text{or} \quad 1 - s_1 > D - \frac{j}{q+1}.$$

This means that for all j,

s_1 is not in the interval $I_j = \left[\dfrac{j}{q+1} + (1 - D), \dfrac{j}{q+1}\right]$.

This is equivalent to saying that the intervals I_j cannot overlap, or that

$$D - 1 < \frac{1}{q+1}, \quad \text{which is the same as } D < 1 + \frac{1}{q+1},$$

contrary to our assumption. So at least one of the $q+1$ strategies $d_1 = j/(q+1)$ gets both nuts, and hence $P^*(D) \le q/(q+1) = 1 - 1/(q+1)$. The result follows by combining the two estimates. ■

Note that in this proof (as in the previous ones), the pilferer's strategy is analysed to show that there is no squirrel strategy that is better than the one we propose.

3.3. Letting D_S, D_P vary

A knowledge of the exact adversarial digging D_P is a rather sharp assumption. Perhaps, we should assume a Bayesian squirrel whose subjective probability gives a distribution on D_P. For example, we might assume for the case $m = n = 2$ and $k = 1$ that we studied earlier, that $D_S = 1$ and total depth D_P dug by the pilferer (or Nature) is uniform on the interval [1,2].

We might further ask how much digging D_S the squirrel allocates from his limited energy resources E, rather than as above taking it as given. The idea is that while increasing his total digging D_S increases his probability of winning the caching game and hence of surviving the winter, the increased effort exerted in digging would lower his conditional fitness, given survival. His fitness would depend on whether or not he survives the winter and, if so, also on his remaining energy. So we might assume a multiplicative fitness function, given the distribution of D_P, of the form

$$F(D_S) = Q(D_S) \cdot O(E - D_S), \tag{3.1}$$

where $Q(D_S)$ is the probability the squirrel survives the winter if he allocates an amount of digging equal to D_S from his energy resources E, and O represents his outside option in the sense of how he could use the energy saved from digging to achieve fitness in other ways. Here, $Q(D_S)$ is not conditional on the value of D_P or any other factors that may contribute the whether or not the squirrel survives the winter. This fitness O is relevant to total fitness only in the case of surviving the winter, hence the multiplicative form. Here, the constant E represents the energy he has available for other activities if he does no digging.

3.4. Diversification: scatter versus larder hoarding

It was shown in Clarkson *et al.* [25] that magpies are more likely to spread out their caches if the risk of cache theft is high. See also Birkhead [49]. We show that this is predicted by a version of our model (propositions 3.1 and 3.2). In this case, there are two sites for caches; so we define the dispersion d of a squirrel strategy as the probability that nuts are placed in both sites. This can be interpreted as the probability of scatter hoarding, considering the use of a single site as larder hoarding. The probability that there is a pilferer in the region (modelling the 'risk of cache theft') is a variable called r. The proofs of these propositions show that (with $D = D_P/D_S$),

$$d = \begin{cases} \frac{1}{3} & \text{if } 1 \le D < 1.5 \\ 0 & \text{if } 1.5 \le D < 2. \end{cases} \tag{3.2}$$

Suppose that the pilferer's digging capacity D_P is fixed at say $D_P = 1$, and the squirrel can choose his digging effort D_S; so $D = D_P/D_S = 1/D_S$. However, there is a cost in fitness that will matter if he survives the winter, so that if he does survive the winter he will have fitness $O(E - D_S) = E - D_S$ (in the terminology of §3.3). We are making the simplifying assumption here that the squirrel cannot use his energy resources E to achieve fitness in any way other than by caching his nuts. Recalling that $P(D)$ is the optimal probability of the squirrel's survival for a given digging ratio $D = D_P/D_S$, the probability $Q(D_S)$, unconditional on D_P, that the squirrel survives the winter is $Q(D_S) = rP(D) + (1 - r)1 = P(1/D_S) + (1 - r)$. If there is no pilferer (probability $1 - r$), this probability is 1. If there is a pilferer, then $P(D)$ is the probability that the squirrel survives, with best play on both sides. Using these expressions for Q and O in (3.1), we obtain the following equation for the squirrel's fitness F as a function of r and his choice variable D_S.

$$\begin{aligned} F(D_S) &= F(D_S, r) \\ &= \left(rP\left(\frac{1}{D_S}\right) + (1 - r) \right)(E - D_S). \end{aligned} \tag{3.3}$$

We must assume that the squirrel can use any amount of energy for digging up to $D_S = E$, so that if he uses all his energy for digging, then he is totally exhausted and dies. Propositions 3.1 and 3.2 say that

$$P(D) = \begin{cases} 1 & \text{if } D < 1, \\ \frac{2}{3} & \text{if } 1 \le D < 1.5, \\ \frac{1}{2} & \text{if } 1.5 \le D < 2, \\ 0 & \text{if } D \ge 2, \end{cases}$$

$$\text{or } P\left(\frac{1}{D_S}\right) = \begin{cases} 1 & \text{if } D_S > 1, \\ \frac{2}{3} & \text{if } \frac{2}{3} < D_S \le 1, \\ \frac{1}{2} & \text{if } \frac{1}{2} < D_S \le \frac{2}{3}, \\ 0 & \text{if } D_S \le \frac{1}{2}. \end{cases} \tag{3.4}$$

So the formula (3.3) becomes

$$F(D_S, r) = \begin{cases} E - D_S & \text{if } D_S > 1, \\ \left(\frac{2}{3}r + (1 - r)\right)(E - D_S) & \text{if } \frac{2}{3} < D_S - 1, \\ \left(\frac{1}{2}r + (1 - r)\right)(E - D_S) & \text{if } \frac{1}{2} < D_S \le \frac{2}{3}, \\ (1 - r)(E - D_S) & \text{if } D_S \le \frac{1}{2}. \end{cases}$$

Clearly it is best for the squirrel to choose D_S either just above 1 (call this 1^+), just above 2/3 (call this $2/3^+$), just above 1/2 (call this $1/2^+$), or equal to 0. So we have

$$F(1^+, r) = E - 1,$$

$$F\left(\frac{2^+}{3}, r\right) = \left(\frac{2}{3}r + (1 - r)\right)\left(E - \frac{2}{3}\right),$$

$$F\left(\frac{1^+}{2}, r\right) = \left(\frac{1}{2}r + (1 - r)\right)\left(E - \frac{1}{2}\right)$$

and $F(0, r) = (1 - r)E$.

So it turns out that the optimal value of D_S is $D_S = 1^+$ if $r > 3/(3E - 2)$, $D_S = 2/3^+$ if $3/(3E - 2) > r > 6/(6E - 1)$, $D_S = 1/2^+$ if $6/(6E - 1) > r > 2/(2E + 1)$ and $D_S = 0$ if $r < 2/(2E + 1)$. Note that in the case that $r > 3/(3E - 2)$, the solution specifies that the risk that there is a pilferer in the area is sufficiently high that the squirrel should optimally bury his nuts completely out of reach of the pilferer. Similarly, in the case that $r < 2/(2E + 1)$, the risk that there is a pilferer in the area is sufficiently low that the squirrel should optimally not bother using any of his energy resources to hide his nuts. We exclude these cases from our attention and suppose that $2/(2E + 1) < r < 3/(3E - 2)$, which, if for simplicity we take $E = 2$, is equivalent to $2/5 < r < 3/4$. Then we see that if $D_S = 2/3^+$, then $D < 3/2$ and by (3.2) the dispersion factor is $d = 1/3$, while if $D_S = 1/2^+$, then $D > 3/2$ and $d = 0$. Taken together, these observations show that $d = 0$ when the risk r of cache theft is relatively small ($r < 6/(6E - 1) = 0.55$ in the case of $E = 2$) and $d = 1/3$ when the risk of cache theft is relatively high ($r > 6/(6E - 1) = 0.55$ if $E = 2$). So in our model, *the squirrels are more likely to spread out their caches if the risk of cache theft is high*, as observed in Clarkson *et al.* [25].

3.5. Digging costs non-additive over sites

Up to this point, we have been assuming the digging effort (energy) required to achieve a given depth is a linear function (energy per unit depth is constant)

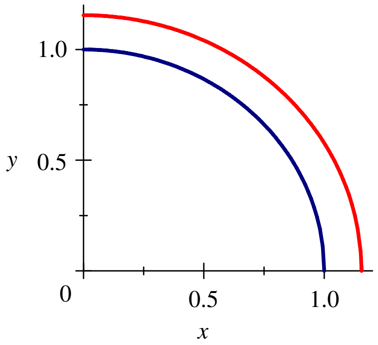

Figure 3. Strategy sets when $D = 4/3$. (Online version in colour.)

and that the energy required to dig to given depths at say two sites is the sum of the energies required at each site (additivity). An anonymous referee has suggested that these assumptions should be relaxed in order to be able to adequately model a wider class of situations. In this section, we show how our techniques can be modified to deal with these relaxed assumptions. We show that our previous analysis, with a suitable interpretation, already deals with nonlinear energy requirements at each site, as long as we make the obvious assumption of monotonicity (deeper holes require greater energy to dig). On the other hand, if the individual energies at sites do not simply add to a total energy requirement, then the game changes and the optimal strategies are different.

We first assume that the energy required to dig to depth d is some digging cost function $c(d)$. Up to this point, we have taken $c(d) = d$, but now we allow c to be any monotone increasing function with $c(0) = 0$ and $c(1) = 1$. For example, if $c(d) = d^2$, so that the digging cost per unit length increases quadratically as you dig deeper, then digging to depths x and y in the two sites would require energy $x^2 + y^2$. This might be exemplified in a soil type that is soft near the top, and harder and more compact deeper down. So in the case of the normal pilferer with two sites and two nuts, the squirrel must choose a vector (x,y) with $x^2 + y^2 = 1$ and the pilferer must choose a vector (x,y) with $x^2 + y^2 = D$. For $D = 4/3$, the strategy sets correspond to the two half circles depicted below in figure 3.

Put another way, the squirrel must choose some $s \leq 1$, corresponding to two holes of depths $(\sqrt{s}, \sqrt{1-s})$ and the pilferer must choose some $p \leq 4/3$, corresponding to two holes of depths $(\sqrt{p}, \sqrt{4/3-p})$. If the squirrel needs one nut to win ($k = 1$), then the pilferer wins if and only if $\sqrt{p} \geq \sqrt{s}$ and $\sqrt{4/3-p} \geq \sqrt{1-s}$, that is to say $p \geq s$ and $4/3 - p \geq 1 - s$. This game is, therefore, equivalent to the original game with $D = 4/3$, which we have already solved in §3.2 and has value $P(D) = 2/3$.

In general, the game played using any digging cost function $c(d)$ as described already can be seen to be equivalent to the original game in which $c(d) = d$. Optimal strategies can be constructed from optimal strategies in the original game, whether the pilferer is normal or smart, by replacing instances of 'dig to depth x' with 'dig to depth $c^{-1}(x)$', and the value $P(D)$ remains unchanged. (Here $y = c^{-1}(x)$ represents the inverse function of c; that is, y is defined by $c(y) = x$.) In the earlier-mentioned example, the squirrel's optimal strategy for the original game with $D = 4/3$ is to choose equiprobably between digging depths (1, 0), (1/2, 1/2) and (0, 1), so that the pilferer can only check at most one of these configurations. If we take $c(d) = d^2$, then an optimal strategy for the squirrel is to choose equiprobably between $(c^{-1}(1), c^{-1}(0))$, $(c^{-1}(1/2), c^{-1}(1/2))$ and $(c^{-1}(0), c^{-1}(1))$—that is (1, 0), $(1/\sqrt{2}, 1/\sqrt{2})$ and (0, 1).

We next consider a situation where digging effort is not additive—that is, it cannot be represented simply as the sum of the digging efforts at the various sites. We take the simplest non-additive model, by imposing a fixed cost C on searching at each site where digging occurs. This could more accurately describe a situation in which a significant amount of energy is required to travel between different sites. For simplicity, we revert back to the assumption that the variable digging effort required in each site is linear in depth, so that digging cost function $c(d)$ is given by $c(d) = C + d$. Thus, the total digging effort required to dig to positive depths d_1 and d_2 at say two sites is given by $2C + d_1 + d_2$, or simply $C + d_1$ if digging only at one site. Suppose we take $C = 1/2$ and once again consider the game where there are two sites and two nuts with a normal pilferer, and $k = 1$. We can no longer take the squirrel's digging, D_S to be normalized to 1, as this would prevent him from digging in more than 1 site. We therefore take $D_S = 3/2$, allowing the squirrel to dig a hole of maximum depth 1 in each site (although he can no longer dig two holes of total depth greater than 1/2). Suppose the pilferer's digging, $D_P = 2$. Then the squirrel's optimal strategy is to hide both nuts at depth 1 in the same site with probability 2/3 at cost $c(1) = 1/2 + 1 = 3/2$, and to hide the nuts in different sites both at depths 1/4 with probability 1/3 at cost $2 \cdot c(1/4) = 2(1/2 + 1/4) = 3/2$. The pilferer can only win against this strategy with probability 1/3, since the cost of digging a hole of depth 1 and a hole of depth 1/4 is $c(1) + c(1/4) = (1/2 + 1) + (1/2 + 1/4) = 9/4 > D_P$. The pilferer can ensure that he wins with probability at least 1/3 by making an equiprobable choice of the three digging depths (1, 0), (1/2, 1/2) and (0, 1). If the nuts are both in the same hole, he trivially wins with probability 1/3, and if they are in different holes neither can be deeper than 1/2, because this would require energy greater than $2C + 1/2 = 3/2 = D_S$; so the nuts are found with probability 1/3 by (1/2, 1/2).

3.6. Pilferer digging energy contingent on success

An anonymous referee has suggested that it would be more realistic to assume that the energy available to the pilferer for digging is contingent on success, so that when the pilferer finds a nut, he can eat it and convert the energy into increased digging potential. This possibility leads to an interesting augmented game $\Gamma^+ = \Gamma^+(D, h)$ (with associated value, or maximin survival probability $P^+ = P^+(D, h)$), in which the pilferer starts with digging potential D but also obtains an additional digging depth h every time a nut is found. So a strategy for the pilferer in the augmented game describes how he will dig as a function of how many nuts he finds. For simplicity, consider the case where the pilferer needs to find two nuts to win—that is, where $k = m - 1$. There are now qualitatively four outcomes:

(i) he finds no nuts before his initial digging potential of D runs out (squirrel wins);
(ii) he finds one nut before D, but no additional nuts with the extra h (squirrel wins);
(iii) he finds two nuts within his initial digging of D (pilferer wins); and
(iv) he finds one nut within his initial digging of D, and one (or more) additional nut with the extra h (pilferer wins).

The first three cases are the same as in the original game Γ, but the last case (iv) is new in the augmented game Γ^+, and this possibility may modify optimal play. In particular, it may mean that placing decoy nuts is no longer optimal for the squirrel. For example, consider the case of the smart pilferer when there are two sites and two nuts, and the squirrel needs one nut remaining to survive ($n = m = 2$, $k = 1$). When $D = 1$, we saw in §3.1 that the solution of the original game Γ was that the squirrel should make an equiprobable choice between three different configurations of the nuts; two of these use a 'decoy nut' to try and trick the pilferer (figure 1). However, for the new game Γ^+, the solution is different if we take, for example, $h = 1/2$, so that if the pilferer finds a nut he is given additional digging depth 1/2. It is now optimal for the squirrel to hide both nuts together at depth 1 at a randomly chosen site, guaranteeing a win (for the squirrel) with probability at least 1/2. The pilferer has an optimal strategy of digging a hole of depth 1, and then if he finds 1 nut, using the extra energy $h = 1/2$ to dig another hole of depth 1/2 in the other site. It is easy to see this guarantees a win for the pilferer with probability at least 1/2, so that the value of the game Γ^+ with $D = 1$ and $h = 1/2$ is 1/2.

Note that for this choice of the parameters m, n, k, D, h the augmented game is essentially the same as if the additional digging effort were given to the pilferer at the start of the game. That is, the solution of the game Γ^+ with $D = 1$, $h = 1/2$ is essentially the same as the solution of the original game Γ with $D = D + h = 3/2$. The squirrel's strategy is the same, the pilferer's strategy is virtually the same and the value of the modified game $\Gamma^+(D, h)$ is the same as that of the original game $\Gamma(D + h)$ in which the pilferer starts with the extra digging potential. Both players play as if they are assuming that the pilferer already has the additional energy $h = 1/2$. In fact, if $1 \leq D + h < 2$, the solution of the game $\Gamma^+(D, h)$ is always essentially the same as the solution of $\Gamma(D + h)$ for this choice of the parameters n, m, k, and this is true for both the smart and the normal pilferer.

In other cases this is not so. For example, consider the original game Γ when there are three sites and two nuts. The analysis for this game has not been included in this paper, but if $2 \leq D < 3$, the squirrel's optimal strategy against the smart pilferer is to bury both nuts at depth 1 in a single site, ensuring a win with probability at least 1/3. The smart pilferer can ensure that he wins with probability at least 2/3 by employing the following strategy. He digs simultaneously at two randomly chosen sites; then if he finds a nut in that site, he continues digging to depth 1 in that site. If he does not find the other nut, he continues to look for it in the third site. Hence, the value of this game is 1/3. However, in the augmented game $\Gamma^+(D, h)$, where $D = h = 1$ (so that $D + h = 2$), the same strategy is not available to the pilferer. In particular, if both nuts are hidden together at depth 1, then this pilferer strategy will find the nuts with probability 0. In fact, the squirrel can now guarantee a win with probability at least 2/3 by using the same strategy of hiding both nuts together at depth 1. The pilferer can ensure he wins with probability at least 1/3 by digging a hole of depth 1 then if he finds a nut, digging two more holes of depth 1/2, so that the value of the modified game $\Gamma^+(D, h)$ is 2/3.

3.7. Effect of 'food value' (parameter k)

It has been shown [50] that caching behaviour depends, to some extent, on the 'value' of the food that is being cached, with higher value foods being cached in more sites (smaller cache size). Their experiments involved Kangaroo rats (*Dipodomys merriami*). In our model, the 'value' of the food can be interpreted in terms of the parameter k, the number of items required for survival. Foods with higher caloric content would correspond to a smaller parameter k. In §3.1, we considered a 'valuable' food source, for which a single ($k = 1$) remaining nut would be sufficient for survival. Under this assumption, we showed in proposition 3.2 that for a range of pilferer digging levels ($D < 1.5$), the optimal caching strategy places the $m = 2$ nuts at two sites with probability 2/3. (The optimal survival probability in this case is 2/3.) For a less valuable food source, where $k = 2$ nuts are required to survive, the solution is simpler. The squirrel strategy of placing both nuts at maximum depth in a random site clearly wins with probability at least 1/2 against any pilferer strategy. Similarly, the pilferer wins with probability at least 1/2 with the strategy of searching a random site to the bottom and the other one to depth $D - 1$. So the optimal survival probability with the less valuable food is 1/2. We have not yet shown that the squirrel cannot behave optimally using both sites. But clearly against the stated pilferer strategy, the squirrel always loses if he uses both sites, as at least one nut will surely be lost. And because the squirrel can win with probability 1/2, any two site caching strategy most be suboptimal. Thus we have shown, in our simple case, that more valuable nuts should be cached at two sites with probability 2/3, while less valuable nuts should never be cached at two sites. We believe that this property, of wider dispersion of more valuable items, persists for larger parameters.

The Leaver & Daly [51] article cites research finding similar effects of food value on dispersion in various animals: red squirrels (*Tamiasciurus hudsonicus*) [51], yellow pine chipmunks (*Tamias amoenus*) [52], grey squirrels (*Sciurus carolinensis*) [53] and heteromyids [54]. The last two cited papers involve the complicating factors of perishability and rarity of the cached food.

3.8. Caching without digging

There is another model that does not involve digging, but only caching. The squirrel has n indistinguishable sites where he can cache a total amount h of a continuously divisible commodity (maybe approximated by small seeds). His 'strategy' is a vector $w = (w_1, w_2, \ldots, w_n)$, with $w_1 \geq w_2 \geq \cdots \geq w_n$ and $w_1 + \ldots + w_n = h$, where the w_i are the weights of material he places, in order of weight. Thus, w_1 is the amount in the largest cache. Suppose he believes that p_z is the probability that of the n sites, z of them will be pilfered completely, where $0 \leq z \leq n$. How should he distribute his material to maximize the probability that he has enough (normalized to 1) to survive the winter? This is an interesting (and unsolved) mathematical problem, even in the apparently simple case that $p_z = 1$ for some known value of z. In that case, the Kikuta–Ruckle conjecture [4] says that the optimal distribution puts equal amounts $w_1 = w_2 = \cdots = w_a = h/a$ in some sites (and nothing in the other sites). Some positive solutions to this conjecture have been obtained in Alpern *et al.* [9] but the general conjecture is still open. This leads naturally to the following ecological question: *Do scatter hoarders typically have equally sized caches*? Also we might ask how the squirrel chooses the number of sites to cache material at.

4. CONCLUSION AND DISCUSSION

In this paper, we have modelled the optimal caching problem faced by a scatter hoarder as a game against Nature that extends the Kikuta–Ruckle accumulation games by adding a 'depth' element to the caching strategy. In a simple model, we determined the randomized caching strategy (involving food distribution and depth at each site), which maximizes, in the worst case, the probability of having enough food left after pilfering to survive the winter. To make the problem tractable, we limited the number of sites available for caching to two, though further work of a more mathematically technical nature can deal with more complex problems. But even our simplified model reveals a number of qualitative results that may have explanatory value for known observations and motivates the search for certain behaviour. For example, we show how the caching strategy requires randomization and is sensitive to the level of threat of pilfering and the food recovery required for survival. We give a further model that shows that optimal play requires the scatter-hoarder to distribute his resources more widely when the threat of pilfering is higher, as found empirically in Clarkson *et al.* [25]. We show the need for the use of 'decoy nuts', placed above other nuts at the same caching site—this can be seen as an experimental prediction that field workers might want to look out for.

Perhaps more importantly, the limitations of our model argue for further modifications so that many interesting relationships can be brought into theoretical view. Some of these are as follows.

- *Variation in critical recovery* (*survival*) *quantity.* In our model, the scatter hoarder's minimum requirement of food is exogenous (given), and was normalized to one. However in the case of corvids, there is evidence that they change their strategy seasonally, caching items quickly and close to the ground in the spring, and investing longer in digging a deeper hole in which to bury the cache in the autumn [55]. So it would seem that a natural extension would be to analyse the dependence of the caching effort D_S on the minimum survival level, which is presumably lower in the spring (because less is needed for summer) than in the autumn (where more is needed in the winter).
- *Multiple food types and perishability.* In our model, there is a single type of resource (all nuts are the same). But, for example, it is observed in Clayton & Dickinson [14] that jays cache both worms and nuts, and keep track of which foods they have hidden where and when. A more robust model would designate which commodity bundles (amounts of worms and nuts) are sufficient for survival. Given this information, a caching strategy would have to consider the caching of both types. To deal with perishability questions, a multi-stage model would be required. First the scatter hoarder hides the worms and nuts, then some pilfering, then some recovery (particularly of the more perishable worms), more pilfering, more recovery.
- *Spacing of caches.* We noted earlier that grey squirrels space their caches further apart if there are fellow grey squirrels in the area [31]. Our model does not consider the geometric configuration of the caching sites. This could be another parameter of the caching strategy. The configuration of sites, especially when search is required to find them again, has been analysed in a related 'find-and-fetch' search game context [56], where the optimal location of a nest in terms of food sources was considered. The search for an immobile target such as a cache has been studied in Gal [57,58]. A related earlier observation that could be brought into such an amended model is that squirrels responded to a reduction in the availability of food by increasing the distance at which they stored the food from the source [32]. A number of studies have found that widely spaced caches are more likely to survive than caches placed close to one another [30,45–47].
- *More information for pilferers.* Our model assumes that the pilferer knows the number and location of the *potential* caching sites, but has no information as to the *actual* burying of the nuts. Considerable work (much of it cited in our review of the scatter hoarding literature) has been carried out in studying how the caching behaviour is affected when onlooking potential pilferers may have partial information

about the initial caching; for example, nuts may be subsequently moved between sites. Such problems cry out for game-theoretic analysis.

The next two items are related to useful comments made by anonymous referees.

— *Continuous dispersal of material over an area.* The assumption of a fixed number of known potential caching locations is rather strong, whereas the weaker assumption that the nuts from a given tree dispersed within a known radius might be more realistic. In this case, a continuous search model might be more appropriate. The possibility of a continuous distribution of resources over a circle has indeed been recently studied in [11], and it is possible that it might be adapted to deal with distributions over a disc (region within a given distance from the tree). The strong assumption made in this paper is in keeping with our 'worst case' analysis of the caching problem as a 'game against Nature'—in fact, the observation that the pilferer might not be able to identify potential caching sites means the squirrel should in fact be able to do even better than our optimal strategies guarantee.

— *Multi-period dynamic accumulation of resources.* Our game model is essentially a single period game, where the squirrel hides nuts and then the pilferer takes some. In fact, the original *accumulation games* of Kikuta & Ruckle were multi-period games, where in each period the squirrel (the hider) hides more nuts and the pilferer comes back again. The game ends positively for the hider if after some fixed number of periods a sufficient amount of material has been saved, or *accumulated* (over time). Such games have proved difficult to solve for more than one period, even as mathematical abstractions, and much of the progress in this direction has been in the one period case (called simply *caching games*). So to apply these models to the dynamic biological setting, further mathematical advances will be required. We hope that our model will stimulate work in that direction. The possibility of recaching (the squirrel moves nuts between locations) should also be allowed in such models.

S.A. and R.F. wish to acknowledge support from NATO Collaborative Linkage Grant 983583.

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