Challenges faced by foraging Eastern grey squirrels, *Sciurus carolinensis*: competition, pilferage and predation risks.

Submitted by Kimberley Jayne, to the University of Exeter
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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signed …………………………………………

Abstract

This thesis examines how Eastern grey squirrels, *Sciurus carolinensis*, modify their foraging and hoarding behaviour in relation to different risks, particularly those which involve a trade-off between securing food resources and avoiding a negative outcome with a competitor. While foraging for food to eat and hoard, squirrels must compete with conspecifics and heterospecifics for access to resources, and they must ensure the safety of their food hoards from onlookers or opportunistic pilferers. While engaging in these behaviours in the most efficient way, they must also avoid being predated upon. Five studies were conducted to further understanding of grey squirrel foraging, hoarding and pilferage behaviours, and how they are affected by different risk factors. The data in this thesis provide experimental evidence that grey squirrels respond directly to conspecific presence as a cue of pilferage risk and adjust their behaviour in ways that may help to reduce cache theft. The data also support the view that conspecific and heterospecific competitors pose risks to foraging and caching, with squirrels modifying their behaviour in ways that serve to avoid negative competitive interactions. Predation risk was found to be particularly disruptive to foraging behaviour, and it also had a seasonal effect upon pilferage rates of experimenter-made caches. A variety of strategies that squirrels might use to pilfer caches were investigated, however, the data did not provide a clear indication of pilferage strategy used by squirrels; they did not seem to use observational spatial memory, and they did not simply pilfer in profitable foraging locations. This thesis raises questions about the mechanisms grey squirrels use to assess pilferage risk and how they engage in pilferage in comparison to other caching species; the studies conducted illustrate different methods that future research could use to investigate food hoarding and pilfering behaviour in wild and captive squirrels.

Contents

Chapter 1: Introduction

Literature review

Chapter 2: The effects of audience and pilferage on caching behaviour in the Eastern grey squirrel: a laboratory study

Introduction

Method

Results

Discussion

Chapter 3: The role of observational spatial learning in cache pilfering by Eastern grey squirrels: a laboratory study

Introduction

Method

Results

Discussion

Chapter 4: Dominance effects on caching in wild Eastern grey squirrels

Introduction

Method

Results

Discussion

Chapter 5: Factors affecting cache pilferage rates at landmarks: predation risk and food availability

Introduction

Method

Results

Discussion

Chapter 6: Behavioural responses of wild Eastern grey squirrels to auditory playbacks of competitors and predators

Introduction

Method

Results

Discussion

Chapter 7: General discussion

Appendices

List of tables

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

List of figures

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Author’s declaration and acknowledgements

The use of the plural “we” has been used throughout Chapters 2 and 6 because these are intended for submission to journals for publication; in addition, because these chapters were written as free-standing papers, there is some repetition between them and other parts of the thesis. However, I can confirm that all the material presented in this thesis is my own work, designed, carried out and written by me, with my supervisors, Lisa Leaver and Stephen Lea, advising on the methods, analysis and drafts of the chapters.

Data from four of the studies in this thesis have also been submitted as theses by four University of Exeter students who were under the supervision of Lisa Leaver and myself for their BSc / MSc dissertation projects: Kirsty Evans for the study presented in Chapter 3, Tom Richards for the study presented in Chapter 4, Frankie Piscitelli for the study presented in Chapter 5, and Frankie Punzi for the study presented in Chapter 6. I can confirm that the methods for the studies were designed before working with the students, whose involvement was to assist with data collection only.

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Manuscripts in preparation

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Chapter 1: Introduction

General introduction

Foraging for Eastern grey squirrels, *Sciurus carolinensis*, frequently occurs within an environment of conspecifics and heterospecifics. While social foraging provides benefits, such as informing about the optimal time and place to forage, it also involves fitness costs to the forager through increased competition and theft of buried food (reviewed in Galef & Giraldeau 2001). Squirrels have been reported to engage in behaviour to help offset these risks, such as adjusting where they forage (Spritzer & Brazeau 2003) or where they cache (Steele, Contreras, Hadj-Chikh, Agosta, Smallwood & Tomlinson 2014), however, such behaviour can be costly to personal safety from predators (e.g., because it involves foraging or hoarding food in more exposed locations). This thesis examines how Eastern grey squirrels modify their behaviour in response to different cues of risk while foraging, hoarding and engaging in pilferage.

The inspiration for this thesis derives from field studies that report that Eastern grey squirrels will adjust their caching behaviour when in the presence of conspecifics or after experiencing food theft, in ways thought to reduce the risk that future hoards will be stolen (Hopewell & Leaver 2008; Hopewell, Leaver & Lea 2008; Leaver, Hopewell, Caldwell & Mallarky 2007; Steele, Halkin, Smallwood, McKenna, Mitsopoulos & Beam 2008). Such ‘cache protection behaviour’ is typically associated with species who are regarded as more cognitively sophisticated, particularly among the Corvidae, with these behaviours possibly indicating that some form of mental attribution is used by cachers and pilferers (reviewed by Clayton, Dally & Emery 2007 and Grodzinski & Clayton 2010). Given that field studies report similar cache protection strategies among some rodents and parids to those observed in corvids, this indicates that these behaviours may not be exclusive to cognitively complex species but common to other caching species. However, far fewer studies have investigated how the social environment affects food hoarding decisions among mammalian scatter hoarders than among corvids.

In addition, recent research indicates that there might be a trade-off between decisions about social risks to foraging and caching, such as cache loss or competing with a more dominant conspecific, with risks of predation (e.g., Steele et al. 2014). While behavioural responses to predation risk have been investigated separately among different species, it is unclear what effect predation risk has in relation to foraging, hoarding and pilfering decisions when social risks are also present. Therefore, research is necessary to establish whether squirrels share similar behavioural strategies with regards to food hoarding as those reported in corvids, as well as how foraging and caching decisions are traded off against pilferage and predation risks. Investigating different combinations of these factors for their effects upon behaviour, as opposed to studying them in isolation, will help to reveal more about how scatter hoarders make their foraging decisions.

Throughout the following literature review comparisons are made between the food storing behaviour of corvids, parids and rodents in order to address questions about the behaviour of the grey squirrel. The theme of these questions relate to specific problems that caching animals encounter while foraging and storing food, including: reducing risk of theft of stored food, how food theft is achieved, competing for resources with conspecifics and heterospecifics, while minimising behaviours that put the individual at increased risks of predation. The optimal conditions of the latter are often in direct conflict with the increased demands of securing food resources, so trade-offs are to be expected. This thesis aims to address some of these questions to determine how squirrels respond to different combinations of cues of risk while foraging and hoarding food. This has been investigated through controlled laboratory studies and field studies presented in Chapters 2 through 6. Comparing grey squirrels with other taxa of food storers will help to understand whether similar adaptive pressures have led to the evolution of similar strategies among different hoarding species for coping with competition, pilferage and predation risks.

Literature review

The foraging ecology of food hoarding animals

Optimal foraging theories concern how the individual could maximise energy intake from foraging, while minimising expenditure (Stephens & Krebs 1986) which can affect where, when, what and how long to forage (Gerber, Reichman & Roughgarden 2004). For species that have evolved a hoarding solution to an environment of “temporal food scarcity”, individuals must compete for seasonal food resources (Roberts 1979), foraging for items such as nuts and seeds when supplies are abundant, and burying them for later consumption during periods of low availability (Vander Wall 1990), while non-hoarders engage in alternative behaviour such as hibernation or migration (Vander Wall 1990). Andersson and Krebs (1978) suggest that the benefits gained from food hoarding (also referred to as ‘storing’ or ‘caching’: Kraus 1983) are dependent upon: the cost of storing; the value of the food item when consumed immediately or stored for later consumption; how likely it is that the stored item will be recovered; as well as costs associated with potential theft of the food hoard.

A number of factors have been reported to affect decisions about food storage. Whether a food item is consumed or cached can depend upon factors which enhance storage time, including the size and weight of the food item (Jansen, Bongers & Hemerik 2004; Jacobs 1992a; Muñoz & Bonal 2011; Preston & Jacobs 2009; Xiao, Zhang & Wang 2004; 2005), and its perishability and germination time (Smallwood, Steele & Faeth 2001; Steele, Hadj-Chikh & Hazeltine 1996). However, consideration of these is beyond the scope of this review. The social environment at the time of foraging can also influence caching decisions. Individuals compete with conspecifics and heterospecifics for the same resources while foraging for food to eat and store, and so they must act in ways that minimise the potential for antagonistic encounters with more dominant competitors, while maximising their foraging effort to offset competition for resources, and ensuring the long-term survival of their caches; this might include transporting food away from locations high in conspecific density (Hopewell et al. 2008; Spritzer & Brazeau 2003). Predation risks are also taken into account when foraging and storing food; individuals act in ways to minimise their exposure to predators, such as foraging or caching closer to trees that might provide an escape route (e.g., Steele et al. 2014). However, the demands of minimising foraging competition can conflict with reducing predation risks, and some studies have indicated that a trade-off might exist but on-going research is needed to establish how these risks interact upon foraging and hoarding decisions.

The focus of the current review will be upon foraging ecology of the eastern grey squirrel. This is a species that has received less attention in the food hoarding literature in comparison to corvids, but some studies have indicated that they could reveal a great deal about food hoarding decision making. This thesis will examine how foraging and caching decisions are made in relation to competition for forageable and stored food, what factors influence pilferage risk, and how trade-offs with predation risk can affect these decisions.

Eastern grey squirrel behavioural ecology

Eastern grey squirrels are among almost 300 species of squirrel worldwide. Within the family Sciuridae they are categorised as tree squirrels due to their native habitat of the hardwood deciduous trees of the North American continent (Steele & Koprowski 2001). They were introduced to Europe in the late 19th century and are now common to urban parklands and gardens in Britain where they thrive (Laidler 1980).

Like most tree squirrels, grey squirrels are not highly social in their diurnal behaviour (Edelman & Koprowski 2007); females only interact with males during spring mating and occasionally related females will sleep in the same nest together for the purpose of thermoregulation during the winter months (Koprowski 1996). They are non-territorial, with overlapping home ranges (Bland 1977; Vander Wall & Jenkins, 2003), and so frequently forage alongside conspecifics (Lewis 1980), particularly during the autumn months when caching rates are high. They demonstrate a variety of complex communication systems which are primarily used for resource guarding (Thompson 1978, 1977) or as alarm behaviours (Lishak 1984), comprising auditory (Horwich 1972; Lishak 1982, 1984), olfactory (Benson 1980; Taylor 1968, 1977; Koprowski 1993) and visual signals. Due to competition for resources, less dominant young grey squirrel males tend to show gradual short distance dispersal to a neighbouring home range (Gull 1977; Thompson 1978). After they have established themselves in a population, they will often show site fidelity remaining in the same area of forest. Female grey squirrels largely show natal philopatry (Koprowski 1996).

Although some species of tree squirrel do hibernate, Eastern grey squirrels instead just become less active over the winter months, reducing their body temperature and energetic needs so they do not need to feed as often (Steele & Koprowski 2001), and will rely on their hoarded food supplies.

Foraging and hoarding of the Eastern grey squirrel

The diet of an Eastern grey squirrel varies seasonally with what is available; in the spring and summer months they feed mainly upon plant material including buds, flowers, shoots and also fungi and insects (Steele & Koprowski 2001), while high nutrition content food supplies are abundant in the autumn when trees drop their nuts and seeds (Long 1995). During the autumn months, grey squirrels spend much of their time scatter hoarding these foods; they disperse single items across many different locations within their home range and rely on these stores to get them through the winter (Jacobs 1989), while preferring to consume more perishable foods while they forage (Hadj-Chikh, Steele & Smallwood 1996). They have been estimated to store around 3000 nuts in a season which are concealed with earth and leaf litter to reduce the likelihood of cache loss to scroungers (Macdonald, 1996).

The following narrative has been adapted from Macdonald (1996), Laidler (1980) and Steele et al. (2008) to describe the typical sequence of behaviours that lead to a cache being made by a grey squirrel. While foraging for food, the squirrel encounters a nut; it will pick it up in its mouth, and manipulate it with its front paws. If the item is selected for hoarding (rather than eating) the squirrel will then usually locomote with the nut in its mouth holding it with its front incisors, often making several stops and sniffing the ground. Sometimes the squirrel will dig at the ground surface material with its front paws but then stop and continue to locomote with the nut in its mouth, and may do this several times. Eventually the squirrel will stop with the nut, while still holding it in its mouth, will dig at the ground, and then deposit the item into the freshly dug hole. The squirrel then uses its front paws and nose to push the nut farther into the excavated site and uses several thrusts of its entire body to ensure the nut is secure. Finally the squirrel will cover the site with soil, plant and leaf litter and pat down the resulting cache with its front paws.

The ontogeny of food hoarding

Little is known about the developmental onset of the behaviours described above, except that it appears to be alike among individual adult squirrels (Horwich 1972). Caching is also widespread among other mammalian species and birds (Vander Wall 1990), particularly members of the corvid family (de Kort & Clayton 2006). Reports from several field and captive studies suggest that storing behaviour appears to be innately triggered but improves with age and experience (Clayton 1992; 1994; Haftorn 1992), cognitive development (Bugnynar, Stöwe & Heinrich 2007; Pollok, Prior & Gunturkun 2000; Zucca, Milos & Vallortigara 2007), and the maturation of memory and physiological brain development (Clayton 1996; Clayton & Krebs 1995). Experience plays an important role in the refining of foraging and storage techniques as the individual matures.

In field observations of tits (crested tit, *Parus cristutus*, willow tit*, P. montanus*), Haftorn (1992) reported that juveniles first engaged in incomplete caching acts while still parentally dependent; for example, attempting to bury items but repeatedly dropping them, or immediately recovering and eating before fully concealing them. Social learning appeared to play very little role in acquisition of the behaviour; storing improved largely with experience alongside foraging efforts, so that juveniles became proficient independent storers before they left the nest. Clayton (1992) reported similar findings in two groups of hand-reared marsh tits, *Poecile palustris;* one was provided the opportunity to cache, the other group was prevented from caching for 24 days after they had become nutritionally independent from their parents. Clayton found that the onset of food storing and retrieving was largely determined by age, and interaction with others was not necessary for developing food storing and retrieval behaviour; acquiring basic storing techniques (choosing suitable storage sites, appropriateness of items stored, the efficiency of and the rate of storing seeds) was mostly affected by the individual’s experience. In a further study Clayton (1994) prevented marsh tits from storing at different ages post-hatching. She found no evidence for a sensitive period for food storing or retrieval; all age groups developed caching with experience of handling food, rather than with age.

In corvids links have been made between the development of food storing and recovery with the Piagetian stages of object permanence (Salwiczek, Schlinger, Emery & Clayton 2009). Object permanence involves an understanding that objects are separate and independent of the observer, and continue to exist even when they are no longer visible (Piaget 1954). Bugnyar et al. (2007) examined how object permanence could be linked to social aspects of development and experience of caching in captive young ravens, *Corvus corax*. They found that behaviour was dependent on age and appeared to develop in hierarchical stages that were associated with Piagetian stages of object permanence. In the first few days after hatching, individuals did not following moving objects (Stage I), but as their visual system developed they begin to visually track an item’s movement (Stage II). Juveniles then started to be able to recover a partially occluded item (Stage III) around the time they would normally leave the nest. Food storing seems to emerge in this stepwise manner so that by around two months post-fledging (Stage IV) they could recover a fully occluded item, demonstrating full adult caching behaviour. Although innately driven, there was also a role of experience during the development of caching behaviour. Progression to Stage V reflected the ability to keep track of multiple covering of caches and recaching, which was affected by experience of caching and recovery. In magpies, *Pica pica* (Pollok et al. 2000), and Eurasian jays, *Garrulus glandarius* (Zucca et al. 2007), improvement in cache retrieval was also linked to experience in Stages V and VI of object permanence, whereby birds could retrieve an item that had been visibly and invisibly displaced from hidden locations.

Less research has been conducted on the development of caching in mammalian hoarders. Smythe (1978) reports observations of week old agoutis, *Dasyprocta punctata*, picking up and attempting to bury small food items that the mother brings to the nest; by about 3 weeks old they are efficient seed buriers making sure that all their caches are fully concealed. Eibl-Eibesfeldt (1963) reports that in red squirrels, *Sciurus vulgaris*, food hoarding behavioural patterns appear stereotyped, even when the individual has no prior experience of digging or handling solid material. In one deprivation study, Eibl-Eibesfeldt hand-reared five young red squirrels taken from the nest and denied them the opportunity to handle any solid particles until 8-10 weeks old. When finally presented the opportunity to handle cachable items, they immediately went through the whole caching repertoire as described above. A further 13 hand-reared squirrels were raised in the same circumstances, except when presented with a cachable item, were prevented from burying it in any substrate. In all of these cases the squirrels went through the first stages of the caching repertoire, up to attempting to push the item into the ground using their nose, and always at the base of a vertical object. In three of the cases, the squirrels went through the entire behavioural repertoire, even including covering the nut with non-existing substrate and patting it down. The caching behaviour of infant grey squirrels also appears to develop along a similar pattern and time scale to that reported by Eibl-Eibesfeldt in red squirrels (personal observations). Although there are systematic reports of the development of caching behaviour among food hoarding mammals, and experience seems to play little role, it would be useful to know whether there are more nuanced influences on particular aspects of caching.

What is apparent among these observations of different caching species is a “motivationally controlled compulsion to cache” (p. 977: Grodzinski & Clayton 2010). While caching is still in its developmental stages, juveniles engage in apparently costly caching behaviour: they attempt to store inedible non-food items (Bugnyar et al. 2007; Eibl-Eibesfeldt 1963), cache in unconcealed locations (Eibl-Eibesfeldt 1963; Smythe 1978), or hide and immediately retrieve items (Bugnyar et al. 2007; Haftorn 1992; Salwiczek et al. 2009). Grodzinski and Clayton (2010) suggest that the key function of these behaviours is to provide the individual with caching experience. These experiences also provide adult cachers the opportunity to learn to incorporate multiple factors into their hoarding behaviour (including: choosing a cache site, dealing with competitors, how to reduce the risk of theft of stored food), so that “an initially compulsive behaviour gradually becomes more flexible and influenced by experience and cognition” (p. 977: Grodzinski & Clayton 2010).

The role for individual experiences and social learning in the development of caching behaviour is perhaps limited, but may become more important in the later acquisition of efficient foraging and storage techniques (reviewed by Galef & Geraldeau 2001). Caching and pilfering experience also play a role in the development of strategies that prevent cache loss in corvids (Emery & Clayton 2001). For example, Bugnyar et al. (2007) reported that experience gained from social interactions during development was important in learning to position caches to prevent stores from being stolen. The influence of the social environment and experience of cache theft upon future food hoarding behaviour is well documented in adult corvids and in some mammals, and will be discussed later in more detail.

Social risks to foraging and hoarding

Foraging for Eastern grey squirrels, as for many animals, frequently occurs within a context of conspecifics and heterospecifics (Koprowski 1994; Leaver et al. 2007; Lewis 1980; Schmidt & Ostfeld 2008; Spritzer & Brazeau 2003). As well as reducing predation risk through dilution (Bednekoff & Lima 1998), reducing the need for increased vigilance (Lima 1995), and informing the individual when it is safe to forage (Galef & Giraldeau 2001), social foraging can benefit the individual by informing when is the optimal time and location to forage through a process of local enhancement (Adams & Jacobs 2007; Heyes, Ray, Mitchell & Nokes 2000). Individuals are frequently more attracted to areas where conspecifics are foraging (reviewed by Galef & Giraldeau 2001): social foraging provides information about where is the optimal place to forage, when to forage (for example, at a previously depleted source that has now recovered), and when to leave the current patch for another. However, the social environment also presents fitness costs to the forager through increased competition for current resources and loss of buried food to theft, ‘cache pilferage’ (Clayton et al. 2007). To ensure optimal energy gain from foraging, grey squirrels have been found to modify their behaviour to offset such costs, as will be discussed in the following sections.

Competing for current resources

Dominance hierarchies can exist at a food patch where individuals of differing social rank compete for food to eat and store (Booth, Gabriel, Joseph & Wafo 2012; Shaw & Clayton 2012a). Within the Paridae and Corvidae social dominance has been suggested to affect food hoarding behaviour in two ways: scatter hoarders compete for access for food to store when they are foraging, and also when they are recovering caches of their own or conspecifics (Clayton et al. 2007). In their game theoretical model, Brodin, Lundborg and Clark (2001) predict that the costs and benefits of hoarding differ between those of different dominance rank. Dominant individuals can use their status to monopolise food supplies, and steal from subordinates, while subordinates tend to avoid engaging in cache pilferage because it could result in an aggressive interaction with those more dominant, and therefore will make more caches and invest more in hiding them since they cannot defend them from dominant thieves.

A number of studies on food storing birds have reported different caching strategies between those of differing social rank. For instance, compared to subordinates dominant birds will use aggression to protect their own caches (Eurasian jay: Bossema 1979; Dally 2004; Goodwin 1956; Wilmore 1977; pinyon jay, *Gymnorhinus cyanocephalus*: Bednekoff & Balda 1996a; raven: Bugnyar & Heinrich 2005; Bugnyar & Kotrschal 2002; Western scrub-jay, *Aphelocoma californica*: Dally Emery & Clayton. 2005a), forage in more preferred locations (willow tit: Hogstad 1988), and supplant others while they are burying food (Eurasian jay: Shaw & Clayton 2012a). Whereas subordinates will suppress caching in the presence of other birds (New Zealand robin, *Petroica australis*: Burns & Steer 2006) opting to cache where there are fewer conspecifics (Eurasian jay: Shaw & Clayton 2012a).

Interspecific dominance hierarchies can also exist at a food patch among individuals that compete for the same resources. For instance, Fisler (1977) observed free ranging California ground squirrels, *Spermophilus beecheyi*, to dominate a food patch visited by a number of competing species (black-throated sparrow, *Amphispiza bilineata*, house finch, *Carpodacus mexicanus*, cactus wren, *Campylorhynchus brunneicapillus*, Gambel's quail, *Lophortyx gambelii*, white-tailed antelope squirrel, *Ammospermophilus leucurus*, Audubon's cottontail, *Sylvilagus audubonii*). Wild Eastern grey squirrels are reported to dominate food patches shared with Eurasian red squirrels (Wauters, Gurnell, Martinoli & Tosi 2001; Wauters, Lurz & Gurnell 2000). Steller's jays, *Cyanocitta steller,* have been observed to rob caches of Clark's nutcrackers, *Nucifraga columbiana* (Tomback 1977). Presence of fox squirrels, *Sciurus niger*, has been found to suppress foraging in Steller's jays (Bekoff, Allen & Grant 1999). In terms of food storing, more dominant species tend to engage in larder hoarding because they can use aggression to defend their stores and pilfer the stores of others (e.g., Ord's kangaroo rat, *D. ordii*, were dominant over Merriam's kangaroo rat, *Dipodomys merriami*: Jenkins 2011; chisel-toothed kangaroo rat, *D. microps*, and Merriam's kangaroo rat were dominant over dark kangaroo mice, *Microdipodops megacephalus*, and long-tailed and little pocket mice, *Chaetodipus formosus* and *Perognathus longimembris*: Jenkins & Breck 1998).

A number of field observations report that grey squirrels have a stable linear dominance hierarchy based around age, so that typically an adult male dominates over younger subordinate males and all females (Flyger 1955; 1960; Horwich 1972; Koprowski 1996; Pack, Mosby & Siegel 1967; Taylor 1966; Thompson 1978); this is maintained for most of the year, with peaks in agonistic interactions during mating seasons (Koprowski 1996; Thompson 1978). Experience, hormonal development and size seem to be important in determining social rank in grey squirrels (Pack et al. 1967); and their dominance relationships are established and maintained through behaviour, as well as visual and olfactory recognition (Horwich 1972).

Few studies have examined how social rank among grey squirrels might affect their foraging behaviour. Allen and Aspey (1986) observed food competition in a group of captive grey squirrels at an experimental food station. They observed five different types of behaviour which they state were indicative of dominance and related to age and sex, all of which were initiated by one squirrel approaching another at a feeder, including fighting, chasing, jumping-at or running at, approach/retreat interactions, and vocalisations. Some research shows that wild grey squirrels might act in ways to avoid competition when foraging in the presence of conspecifics, such as transporting food away from a food patch (Spritzer & Brazeau 2003), increasing vigilance levels to identify potential competitors (Tarigan 1994), and responding to the auditory presence of conspecifics with alarm behaviour (Partan, Fulmer, Gounard & Redmond 2010; Partan, Larco & Owens 2009).

Examining dominance hierarchies is further complicated when food hoarding is also involved; the social environment may affect an animal's ability to ensure the safety of buried food stores. For instance, Spritzer (1999) reports anecdotal observations of squirrels aggressively defending their caches. To our knowledge there is only one study of grey squirrels that suggests there might be a link between social rank and individual differences in caching behaviour. Leaver, Martin and Romaine (unpublished data) found that dominant individuals would cache differently to subordinates, with more dominant grey squirrels clumping their caches while submissive individuals distributed their caches more widely. From this study it seems that caching behaviour in grey squirrels is affected by social dominance; possibly because higher ranking individuals may be more able to aggressively defend their caches, whereas subordinates may need to rely on other pilferage avoidance mechanisms. Further research would help to establish more clearly whether there are individual differences in the hoarding behaviour of grey squirrels based upon dominance, and by what mechanisms individuals use to ensure the survival of their caches.

Minimising the loss of future resources

Theft of hoarded food can be costly to scatter hoarders who are unable to defend their individual caches from pilferers. Estimated levels of cache pilferage vary considerably: Vander Wall and Jenkins (2003) reviewed natural and artificial cache pilferage rates in a number of caching species and suggest that rates for most long term hoarders probably fall between 2-30% per day; though the upper end of this range has been challenged by Leaver et al. (2007). Andersson and Krebs (1978) argue that for food hoarding to be an evolutionary stable strategy the cacher must have a recovery advantage of its own stores. However, others argue that caching behaviour can be adaptive even in an environment of food theft and that some species are able to tolerate cache theft by engaging in reciprocal pilferage (Smulders 1998; Vander Wall & Jenkins 2003). Within these systems individuals invest in their own food stores but also pilfer caches made by conspecifics; caching remains an evolutionary stable strategy because the hoarder is more likely to recover their own stores, but pilferage is tolerated because both hoarders and thieves can benefit from buried food. Models of reciprocal pilferage systems report pilferage tolerance as particularly high for small solitary animals that have overlapping home ranges, such as within the Rodentia and Paridae (Smulders 1998; Vander Wall & Jenkins 2003). The following section will examine research which has shown how cachers minimise the loss of their food stores to thieves and enhance their recovery successes. Later, the discussion will consider strategies used by pilferers to enhance their ability to locate caches made by conspecifics.

Research has shown that a wide range of food hoarding species engage in behaviour that might help to minimise the risk of cache loss to competitors, indicating that actively attempt to avoid pilferage. For instance, after experiencing pilferage of their caches birds and rodents have been reported to engage in behaviour to help reduce future loss, including: re-locating caches (Merriam’s kangaroo rat: Preston & Jacobs 2005; Western scrub-jay: Dally Emery & Clayton 2005b), recovering and eating caches (Western scrub-jay: Emery et al. 2004), avoiding future caching in pilfered locations (black-capped chickadee, *Parus atricapillus*: Hampton & Sherry (1994); marsh tit: Stevens 1984), spacing caches farther apart (Pere David’s rock squirrel, *Sciurotamias davidianus*, Korean field mouse, *Apodemus peninsulae*, striped field mouse, *Apodemus agrarius*, Chinese white-bellied rat, *Niviventer confucianus*, and rat-like hamster, *Tscherskia triton*: Huang, Wang, Zhang, Wu & Zhang 2011), and reducing caching and increase eating (Pere David's rock squirrel: Luo, Yang, Steele, Zhang, Stratford & Zhang 2014). Furthermore, compared to when caching alone, storing food in the presence of other hoarders can result in a higher degree of cache theft (e.g., Steller's Jay, (*Cyanocitta stelleri*: Burnell & Tomback 1985; nuthatch, *Sitta europaea*: Carrascal & Moreno 1993; marsh tit: Sherry, Avery & Stephens 1982). As already discussed in the previous section, dominant pilferers can supplant cachers while they are storing food by using their physicality, but, as will be examined later, sometimes onlookers can return to cache sites to pilfer after the cacher has left the area which helps to avoid confrontation with the cache owner. Some species are sensitive to social information at the time of caching and will adopt different strategies to help to minimise the risk of cache loss when storing in the presence of conspecifics (for reviews of social factors implicated in caching behaviour see: Brodin 2010; De Kort, Tebbich, Dally, Clayton et al 2006).

Many studies that have investigated how food hoarders modify their caching behaviour in response to social cues have been conducted with social species of corvids and parids. When storing food in the presence of conspecifics, many hoarders engage in behaviour that serves to reduce the risk of theft of their stores. Some of these behaviours in food storing birds include: caching less in the presence of observers and more when alone (Clark's nutcracker: Clary & Kelly 2011; coal tit, *Parus ater*: Brotons 2000; black-capped chickadee, *P. articapillus*: Stone & Baker 1989; Eurasian jay: Goodwin 1956; grey jay, *Perisoreus canadensis*: Burnell & Tomback 1985; magpie: Clarkson, Eden, Sutherland & Houston 1986; Northwestern crow, *Corvus caurinus*: James & Verbeek 1984; rook, *C. frugilegus*: Simmons 1968; Western scrub jay: Dally et al. 2005a; willow tit: Alatalo & Carlson 1987; Lahti & Rytkonen 1996), eating more in the presence of observers (nuthatch: Carrascal & Moreno 1993; rook: Dally, Clayton & Emery 2008), and delaying the onset of caching when in the presence of observers (black-capped chickadee: Stone & Baker 1989; magpie: Clarkson et al. 1986; raven: Bugnyar & Kotrschal 2002; Heinrich & Pepper 1998). Several species of corvid and some parids also exploit visual aspects of their environment when caching in front of observers, such as caching behind visual barriers (raven: Bugnyar & Heinrich 2005; Bugnyar & Kotrschal 2002; Heinrich & Pepper 1998), storing in difficult-to-see areas (magpie: Clarkson et al. 1986; mountain chickadee, *Poecile gambeli*: Pravosudov 2008; Western scrub jay: Dally, Emery & Clayton 2004; 2005b), or at a greater distance from observers (coal tit: Brotons 2000; Western scrub jay: Dally et al. 2005b). They will also return to caches and re-bury them in new locations (Clark's nutcracker: Clary & Kelly 2011; Eurasian jay: Cramp & Perrins 1994; Goodwin 1955; 1956; raven: Bugnyar & Kotrschal 2002; Heinrich 1999; Western scrub-jay: Dally et al.

2005a; Emery & Clayton 2001; Emery, Dally & Clayton 2004; Thom & Clayton 2013).

Much research shows pilferage-reduction behaviours are common to scatter hoarding birds that live within large social groups, where competition and the opportunity to steal after observing an individual cache are high, particularly those within the families Corvidae and Paridae. However, some studies have demonstrated that non-social species keep track of social cues while food hoarding. For example, Clark’s nutcracker's showed reduced levels of caching while being observed, and would recover and eat or re-cache more food items after being observed storing (Clary & Kelly 2011). Other evidence of pilferage avoidance behaviour among non-social species come from studies of mammalian food hoarders. Clarke and Kramer (1994) found that scatter hoarding Eastern chipmunks, *Tamias striatus*, change their caching locations depending upon the number of conspecifics at a food patch, which could help to reduce cache pilferage. Merriam’s kangaroo rats dig up their caches and rebury them when an observer is no longer present (Jenkins & Peters 1992). Even for less social species, foraging alongside conspecifics and heterospecifics is common when they depend upon the same resources. While there can be benefits to foraging alongside others (as already noted) for species that are less social, often the fitness costs, such as food theft, can outweigh the benefits. Therefore, engaging in behaviour to offset these risks, such as pilferage avoidance behaviour, when in the presence of potential competitors does not appear to be exclusive to social species, but these behaviours may be common to other scatter hoarders that do not develop within an exclusively social environment (Clary & Kelly 2011).

Links have been made between the sophisticated cognitive abilities of corvids and some of the cache protection behaviour in which they engage; a key topic of research among those who study food storing corvids. When corvids have demonstrated some types of pilferage avoidance behaviour, researchers have argued that the behaviour is a form of prospective cognition. For instance, anti-pilferage behaviour (e.g., caching using a visual obstruction) has been argued as possible evidence that some form of mental attribution, such as perspective taking, is used by cachers; and that individuals are anticipating and responding to the potential pilferage of their caches (discussed in Clayton et al. 2007 and Grodzinski & Clayton 2010). Clayton (2007) suggests that a high degree of social cognition and general intelligence, as well as a relatively large brain with expanded avian prefrontal cortex, allows for the presence of these types of behaviour in some corvids.

Nevertheless, cache protection behaviour has been reported in a number of mammalian cachers that are not usually considered to be as cognitively sophisticated as corvids. When in the presence of observers, individuals have been found to cache less (Norway rat, *Rattus norvegicus*: Denenberg 1952; Miller & Postman 1946), cache more, possibly to offset cache loss (Korean field mouse: Zhang, Wang & Zhang 2011; white-footed mouse, *Peromyscus leucopus*: Sanchez & Reichman 1987), disperse caches more widely (Pere David's rock squirrel, Korean field mouse, striped field mouse, Chinese white-bellied rat, and rat-like hamster: Huang et al. 2011; Eastern chipmunk: Clarke & Kramer 1994), and re-cache when the observer is no longer present (Merriam's kangaroo rat: Jenkins & Peters 1992). Therefore, engaging in pilferage avoidance behaviour in response to social cues does not appear to be something that is exclusive to more cognitively complex species but common to other caching species. However, whether individuals are simply responding to the presence of conspecifics as cue to the risk of cache pilferage, or whether mental attribution processes are involved, like has been argued about corvids, is not fully understood in mammalian food hoarders.

More evidence of audience effects upon food hoarding in mammals comes from field observations of Eastern grey squirrels. Though these are not a highly social species because they do not live in groups (Koprowski 1996), they are likely to benefit from engaging in cache protection behaviour due to the environments in which they forage, principally food patches that attract a high density of conspecifics during the peak caching season. Furthermore, they do not willingly share their food hoards with kin (Spritzer & Brazeau 2003) or conspecifics (Leaver et al. 2007). Tree dwelling species of squirrel also rely heavily on their visual system in comparison to other rodents (Van Hooser & Nelson 2006), and grey squirrels have a wide visual field (Kaas, Hall & Diamond 1972) and excellent spatial acuity (Jacobs, Birch & Blakeslee 1982) which could facilitate monitoring their social environment. These behavioural and morphological characteristics indicate that they may benefit by responding to social cues with pilferage avoidance behaviour.

Hopewell and Leaver (2008) found that wild Eastern grey squirrels in the UK were sensitive to the presence of conspecifics when caching their food and performed behaviours that may help to prevent cache pilferage. In particular, when in the presence of other squirrels, the subjects would: show more vigilance; delay the start of their caching behaviour after collecting a nut; spend more time disguising their caches with leaf litter, especially when caching a preferred item; and made more interruptions to caching, particularly when storing preferred items. Further field studies by Leaver and colleagues report that grey squirrels will cache less in the presence of observers and more when alone, turn their backs to conspecifics while caching, space their caches farther apart (Leaver et al. 2007), and will transport food items and cache them at farther distances from the food source when there are competitors around, and especially when food availability is low (Hopewell et al. 2008).

In the USA, Steele et al. (2008) report that in the presence of observers wild Eastern grey squirrels will eat more, store food in locations with less visual access and make more interruptions to their caching. Steele and colleagues also report the frequent occurrences of an interesting behaviour which they call ‘deceptive caching’. Steele, et al. describe a typical caching episode by a squirrel (digging a hole, appearing to push a nut into the hole, and covering the site with soil and patting down the cache), however, at the end of the suite of behaviours the squirrel exits the site still nut carrying. They suggest that squirrels do this to deceive those individuals that may be watching to reduce the risk of cache pilferage. Leaver et al. (2007) suggest that studies such as these supports the idea that squirrels may also possess more complex cognitive abilities like those found in many corvid and some parid species; however, efforts to mislead conspecifics in this way have not been observed in studies of grey squirrels in the UK (Hopewell & Leaver 2008). Indeed, if ‘deceptive caching’ was intentional, this type of behaviour is more characteristic of species that demonstrate highly sophisticated cognitive abilities, and has been reported in some corvids (raven: Bugnyar & Kotrschal 2004; Heinrich 1999; rook: Seed, Emery & Clayton, personal observation in Dally, Clayton et al 2006). While Steele and colleagues (2008) do acknowledge that it would be premature to suggest that the nature of the deceptive caching they report is ‘cognitively tactical’, the behaviour, nevertheless, is consistent with some of the definitions of tactical deception, and qualifies as a behaviourally deceptive and an adaptive ‘pilferage-averting behaviour’. Though sensitive to the social context, Steele et al. note that further detailed and controlled studies are needed to clarify what specific cues cachers respond to when engaging in behaviour to reduce pilferage, and understand the triggering factors of this type of behaviour among squirrels.

Furthermore, grey squirrels have been shown to be sensitive to heterospecific presence in the context of potential cache theft. Steele et al. (2008) found that after witnessing a human pilfer their recently made cache, wild squirrels would react by caching out of view or eating more nuts rather than caching them. However, as this study does not represent an ecologically relevant risk to caches, namely pilferage by a human, this might indicate that squirrels are simply responding to cache loss, as opposed to witnessing the theft of their caches. Further studies that aim to isolate experience of cache loss from social cues of pilferage would help to clarify how squirrels might be assessing pilferage risk, and elucidate whether they assess risks to caching in a similar way to corvids.

There is some evidence to suggest that corvids might pose a risk to the caches of grey squirrels. Vernelli (2013) observed magpies follow grey squirrels and pilfer their newly made caches. Some species of corvid also possess observational spatial memory and so are able to return to pilfer caches some time after the cacher has left the area (this will be discussed in more detail later). Two studies have directly investigated the risks that corvids pose to grey squirrel caches and reveal seemingly incompatible results. When playbacks of blue jay, *Cyanocitta cristata*, vocalisations were played to wild caching grey squirrels, they reduced their foraging effort when recovering caches, compared to retrieving caches they made in the absence of the playbacks (Schmidt & Ostfeld, 2008). However, grey squirrels do not appear to engage in the same anti-pilferage behaviour at the time of caching in the presence of corvids compared to when caching in front of a conspecific audience. In field observations squirrels were found to make more caches while alone, bury caches farther apart in the presence of conspecifics, and face away from other squirrels while burying food but not while caching in the view of corvids (Leaver et al. 2007). Given that corvids can fly to observe a cache being made, it is possible that engaging in pilferage avoidance behaviour would not benefit a caching squirrel. However, whether heterospecifics pose similar risks as conspecifics to foraging and caching grey squirrels requires further investigation.

Using pilferage as an effective foraging strategy

Throughout periods of low food availability, scatter hoarding birds and mammals must recover large numbers of their scattered caches. As has been discussed, individuals engage in behaviour to offset the risk of cache loss to thieves. However, given that pilferage is a problem for many species of hoarder, how do cachers ensure they have a good chance of recovering their own stores, and how do thieves increase their pilfering success? Bugnyar & Kotrschal (2002) argue that there is an ‘evolutionary arms race’ between cachers and the pilferers: within species, the ability for cachers to engage in cache concealment behaviour has evolved alongside ways that pilferers increase their potential for stealing a cache. The following sections will examine two strategies that scatter hoarders use to recover their stores, namely spatial memory and visual cues. In respect of each, it will be examined how cache thieves may also take advantage of using similar strategies to increase their pilferage efforts beyond random search.

Strategy 1: Spatial memory

Spatial memory plays an important role in the behaviour of many scatter hoarding birds and some scatter hoarding mammals in recovering their own food stores (for reviews see: Sherry 1992; Shettleworth 1990; Smulders, Gould & Leaver 2010). Some birds can recover their caches with a great degree of accuracy and after an extended period of time (Clark's nutcracker: Kamil &

Balda 1985; Tomback 1980: Vander Wall 1982; Vander Wall & Hutchins 1983; Eurasian nutcracker, *Nucifraga caryocatactes*: Conrads & Balda 1979; pinyon jay, *Gymnorhinus cyanocephalus*: Balda & Kamil 1989; Romonchuk 1995; raven: Heinrich & Pepper 1998; magpie: Feenders & Smulders 2011; coal tit: Male & Smulders 2007a; marsh tit: Sherry, Krebs & Cowie 1981; Shettleworth & Krebs 1982; black-capped chickadee: Sherry 1984). However, compared with birds, mammals can rely more heavily on olfactory cues to locate their stores so they may have less need to use spatial memory. Nevertheless, when comparing the use of spatial memory over olfactory cues, mammalian cachers benefit from spatial memory to locate their stores compared to those using random olfactory search (Merriam's kangaroo rat: Jacobs 1992b; pine chipmunk, *Tamias amoenus*: Vander Wall 1991, 2000; deer mouse, *Peromyscus maniculatus*: Vander Wall 2000; for reviews of rodents using memory to recover caches see: Smith & Reichman 1984; Smulders et al. 2010). Remembering the location of buried caches, as opposed to simply relying on olfaction, is critical for the survival of scatter hoarding grey squirrels. This species are active all winter in climates where caches are frequently under snow for several weeks, making it more difficult for them to be recovered using olfactory information (Lewis 1980). Experimental studies demonstrate that grey squirrels can use spatial memory to recover their own caches (Jacobs & Liman 1991), and that they prefer to use spatial and visual information (discussed later) over olfactory cues for recovering artificial caches (McQuade, Williams & Eichenbaum 1986). Moreover, Macdonald (1997) suggests that the spatial memory of grey squirrels is accurate enough to use in cache recovery.

In relation to cache pilferage, some species can also learn and remember the locations of caches that they have seen others make, an ability that requires a highly accurate observational spatial memory (OSM). This can be used to increase pilferage success, and may be a more efficient strategy than random olfactory search, and it is safer than immediately pilfering a cache because the cache owner might still be in the area (Clayton & Emery 2009). A number of species of birds and rodents have been observed to pilfer a few minutes after a cache has been made (magpie:Vernelli 2013; raven: Bugnyar & Kotrschal 2002; Schied & Bugnyar 2008; black capped chickadee: Baker, Stone, Baker, Shelden, Skillicorn & Mantych 1988; Hitchcock & Sherry 1995; Eastern grey squirrel: Steele et al. 2014; Merriam's kangaroo rat: Daly, Jacobs Wilson & Behrends 1992; North Island robin, *Petroica longipes*: Armstrong, Garland & Burns 2012), however pilfering by observation has the risk of the cacher still being close. Using OSM allows the pilferer to return to caches at will after the cacher has left the area, and has only been experimentally tested and found in a few corvids and one parid: Mexican jays, *Aphelocoma ultramarina*, and pinyon jays return to efficiently pilfer caches after a delay of 1-2 days (Bednekoff & Balda 1996a; 1996b), Western scrub jays can pilfer after a four hour retention interval (Griffiths, Duart & Clayton, unpublished data in Clayton, Griffiths, Emery & Dickinson 2001; Watanabe & Clayton 2007), and great tits, *Parus major*, can accurately locate caches made heterospecifics after a 24 hour interval (Brodin & Urhan 2014).

Some species are reported to have highly accurate spatial memory but perform poorly in OSM tasks that require longer retention intervals than a few minutes (e.g., black-capped chickadee: Baker et al. 1988; Hitchcock & Sherry 1995; Sherry 1984). The presence of OSM among some species, but not others, has led some researchers to suggest that the ability to locate conspecifics' caches has a basis in social cognition (Heinrich & Pepper 1998). OSM has a strong cognitive component, such as the requirement for an understanding of object permanence and delayed local enhancement (discussed in Scheid & Bugnyar 2008). Within the 'evolutionary arms race', the propensity to develop strategies for protecting caches and experiencing or engaging in pilferage depends upon opportunities for social learning, and thus may be influenced by group living (Dally, Clayton et al. 2006). Thus, Bednekoff & Balda (1996b) suggest that for non-flocking species such as the Clark's nutcracker who perform less well in OSM tests, despite being a specialised cacher, the opportunities for watching another bird may be relatively infrequent compared to highly social pinyon jays or Mexican jays who demonstrate longer retention intervals, and this may be related to the degree of development of observational learning abilities. An alternative viewpoint has also been suggested for why some caching species possess OSM while others do not. When Scheid & Bugnyar (2008) compared ravens (socially dynamic cachers), against jackdaws, *Corvus monedula* (socially cohesive but cache less), for retrieving cached food items, jackdaws performed less well compared to the ravens. They suggest that observational memory abilities might be more connected with how much the species relies on caches for food, rather than simply social life. In this regard, it is possible that OSM has evolved as a consequence of social living but in combination with cache dependence (Bednekoff & Balda 1996b). However, a recent study reporting the proficient cache locating abilities of a non-hoarding species, the great tit, at recovering caches made by marsh tits does not support this viewpoint. More studies on a wider a range of caching species that vary in their dependency upon caches, and differ in their sociality would help to further an understanding of this.

Though some corvids use OSM to pilfer caches, very little is known about pilfering behaviour in general among food hoarding species: the majority of studies investigate artificial experimenter-made caches as a measure of pilferage rates, particularly in wild studies because it difficult to monitor true cache pilferage (Vander Wall & Jenkins 2003). Grey squirrels are a suitable candidate to further investigate OSM in cache pilferage. Squirrels appear to be sensitive to their social environment, and might be engaging in socially and cognitively complex behaviour when ensuring the safety of their caches in a similar manner to corvids. They are predominantly asocial but forage and cache where there are competitor conspecifics and heterospecifics, and they can use spatial memory to locate their own caches. Further research would clarify what cues are used during cache pilferage and whether conspecific audiences do pose a risk to caching squirrels, as well as whether a specialist non-corvid caching species can also OSM to pilfer. On the other hand, if squirrels did not use observational spatial memory to pilfer caches then this would pose further questions of how squirrels engage in cache pilferage; an alternative strategy is discussed next.

Strategy 2: Visual cues

Scatter cachers have been reported to remember the spatial location of their stores and make use of visual cues and landmarks as beacons to aid cache recovery and locate experimenter or conspecific made caches. A number of captive experiments and a few field observations report the use of landmarks as beacons by corvids and parids during caching and recovery. Captive Clark’s nutcrackers have a preference to cache close (within 5cm) to large conspicuous objects (Vander Wall, 1982); the more visual cues that are available the fewer errors they make when recovering their stores (Kamil, Goodyear & Cheng 2001); and when visual cues close to cache sites have been moved or removed they have difficulty retrieving their stores (Balda & Turek 1984; Gould-Beierle & Kamil 1996). Studies of captive black-capped chickadees similarly report that the removal of visual landmarks from their enclosure resulted in reduced recovery accuracy (Cheng & Sherry 1992; Duff, Brownlie, Sherry & Sangster 1998; Herz, Zanette & Sherry 1994). Adding visual cues close to cache sites increased recovery accuracy for captive grey jays compared to when there were no cues (Bunch & Tomback 1986). In the absence of other spatial information, or when misleading spatial information is presented, captive Western scrub jays and magpies use visual cues to retrieve food (Feenders & Smulders 2011; Watanabe 2005). Wild European jays, *Garrulus glandarius*, use nearby objects to locate cached food, show a preference for using objects that stand out from their background in terms of colour, and prefer vertical to horizontal beacons (Bossema 1979).

Some scatter hoarding mammals also use visual cues when they cache food, and are better at recovering their stores when visual cues are available (Merriam's kangaroo rat: Barkley & Jacobs 1998; Mongolian gerbil, *Meriones unguiculatus*: Collett, Cartright & Smith 1985; Southern flying squirrel, *Glaucomys volans*: Gibbs, Lea & Jacobs 2007; laboratory rat: Olton & Samuelson 1976; yellow pine chipmunk: Vander Wall 1991; Vander Wall, Briggs, Jenkins, Kuhn, Thayer & Beck 2006), and are better at recovering their caches compared to when they just use random olfactory search (Merriam's kangaroo rat: Jacobs 1992b; pine chipmunk: Vander Wall 1991; 2000; deer mouse: Vander Wall 2000; for reviews of rodents and other mammals using memory to recover caches also see: Smith & Reichman 1984; Smulders et al. 2010; Sherry 1985). Captive Eastern grey squirrels have been shown to use visual cues to recover their own caches, and are surprisingly accurate at doing so despite their caches being close to those made by other squirrels (Jacobs & Liman 1991). McQuade et al. (1986) demonstrated that grey squirrels preferentially use extrinsic cues (visual and spatial information) over olfactory cues to locate experimenter made caches. McQuade et al. trained wild-caught squirrels to associate three different and distinct cues with a seed reward contained in a petri dish: olfactory cues (flower extracts on the covers of the petri dish), visual cues (coloured tape covering the dish), and spatial cues (a 3x4 spatial arrangement of the dishes around the arena), and found that squirrels showed a preference for visual and spatial cues when provided the opportunity to recover from all types of cue simultaneously. It is much more difficult to study natural cache recovery in the wild, with researchers still opting for experimenter-made caches: in one such study, grey squirrels were found to locate caches with 62.5% accuracy after a delay of 20 days using visual cues; in comparison, red squirrels (who are less reliant on scattered caches for survival) were far less accurate (Macdonald 1997). These studies demonstrate that landmarks can be used as beacons and illustrate the critical role that they can have upon the caching decisions and recovery success and discovery of caches in a variety of food hoarding species.

Some researchers have argued that the use of visual cues during caching gives cachers a recovery advantage over cache pilferers (McQuade et al. 1986). However, if we return to the argument presented by Bugnyar & Kotrschal (2002), that cachers and pilferers are in an evolutionary arms race, given that cachers have evolved ways to more efficiently locate their own caches (i.e., using visual cues), it is possible that pilferers of the same species (who possess the same cache retrieval mechanisms) might have evolved similar cache pilfering mechanisms alongside cachers; that is to say, food thieves might use visual cues to increase their pilfering success. This is an idea that has not been empirically tested, though some studies do indicate that this behaviour could be likely for cache pilferers. For instance, Vander Wall (1982) reported that Clark's nutcrackers preferentially searched near objects, where caches were more concentrated, to recover caches that they had not made themselves. The studies mentioned above of grey squirrels used caches that the squirrels had not made themselves to measure cache recovery using impermanent features and reported squirrels as accurate at retrieving these caches (McQuade et al 1986; Macdonald 1997). For wild rural and urban grey squirrels the most useful visual cues are likely to be vegetation, such as trees and shrubs, as well as manmade fixtures. In wild jays, Bossema (1979) reported the use of "vertical structures such as saplings and tree trunks" (p. 1). Some studies report that artificial caches made closer to the base of trees are stolen at higher rates in locations that are frequented by grey squirrels (Leaver, Jayne & Lea 2014; Steele et al. 2014), however the precise reason for this is not clear. It is possible that caches are more vulnerable to pilferage under trees because the tree acts as a beacon to both cachers and pilferers of the whereabouts of hoarded food, as indicated by Bossema. However, it is also possible that many animals spend more time foraging under the cover of trees because there is generally more food in these locations and they offer an escape from predators, naive competitors happen upon caches more often closer to trees. Further research of this type would help to provide insight into the cues that squirrels, and hoarders in general, use when engaging in cache pilferage and also when deciding where is the optimal place to store food in terms of cache longevity.

Predation risks while foraging and hoarding

According to optimal foraging theory, the goal of the foraging animal is to maximise the rate at which energy can be acquired from the environment, while using the least amount of time to acquire a given amount of energy. Foraging decisions, such as where and when to eat or hoard, require a trade-off between these two conflicting goals (Sinervo 2006). The preceding discussions have highlighted how risks posed by conspecific, and sometimes heterospecific, competitors can affect whether the individual is foraging and hoarding optimally, and ultimately the long term survival of the individual. However, the costs and benefits of social foraging become more complex when the costs of predation are taken into account, and there appears to be a multi-way trade-off between these decisions. Predators pose a more direct risk to the fitness of foraging animals and therefore greatly impact their foraging decisions. While foraging, animals assess risk and change their behaviour to lower their probability of being predated (Lima & Dill 1989). However, behavioural strategies which lessen predation risk are often at odds with behaviour to maximise efficient foraging and hoarding (Valone & Lima 1987): for instance, there is a trade-off between efficient feeding (choosing to eat at a patch) and exposing oneself to increased predation risk. Moreover, areas with higher risks of predation might be the optimal places to forage and store, potentially due to less competition by other foragers; though further research is necessary to explore how they are traded-off against one another. The following discussion will examine what is already known about grey squirrel foraging behaviour and how it changes under predation risk. It will then go on to explore the role of predation risk in hoarding efficiency, separate from the topic of general foraging, and how there might be a trade-off between predation risk with risks posed by competitors and pilferers.

The effect of predation risk on foraging behaviour

Tree squirrels, which include grey squirrels, inhabit wooded rural and urban areas, making use of trees for both feeding and safety. While they spend much of their time foraging close to trees for fallen nuts and seeds, they often have to travel beyond the cover of the tree canopy in order to locate more resources as food becomes scarce in their current patch (Lima, Valone & Caraco 1985). Foraging at an increased distance from tree canopy can put the individual at greater risk from both aerial and terrestrial predators (reviewed in Verdolin 2006). Grey squirrels are well adapted to respond to cues of predation; they are fast and agile while on the ground as well as in the trees, and use a combination of senses to monitor for the presence of predators. They can use olfactory information from predator scent marks, such as droppings and urine, to help to determine how recently the predator was in the vicinity, reducing their foraging time in locations where a predator has been recently, and thus reducing their exposure to risk (Booth et al. 2012; Müller-Schwarze 2009). They monitor for visual and auditory alert behaviour from nearby conspecifics which may indicate predator presence, and respond to these by increasing their vigilance (Lishak 1984; Partan et al. 2010; Partan et al. 2009). While some animals interrupt their feeding in order to visually scan their environment for potential predators, squirrels can benefit from bipedal vigilance while continuing to eat or handle food; they use this to obtain information about the environment, and will spend more time being vigilant if their view is obstructed (Makowska & Kramer 2007). What is more, grey squirrels actively engage in various behaviours directly aimed towards predators, such as using tail signals, “flagging”, (Partan et al. 2010; Partan et al. 2009) or vocalisations (Lishak 1984) to ward them off, though these are often performed at a high cost to foraging (Makowska & Kramer, 2007; Shonfield, 2011).

There is an extensive literature exploring how predation risk affects foraging decisions (reviewed in Verdolin 2006), however focus here will be on research that has been carried out with squirrels. The risk of predation is powerful in shaping the foraging strategies of squirrels, affecting where they forage and for how long. At artificial food patches, fox squirrels (Brown Morgan & Dow 1992), chipmunks and grey squirrels (Bowers, Jefferson & Kuebler, 1993) feed less in exposed areas away from tree canopy. When foraging in areas farther from cover, grey squirrels eat and handle the same quantity of seeds faster than in areas of safety (Newman, Recer, Zwicker & Caraco, 1988). Flight initiation distance, the distance at which they begin to flee if exposed to a predator, increases as they become farther away from refuge (Dill & Houtman, 1989). Squirrels reduce their foraging time in locations that have cues of predator presence, including odours (Booth et al. 2012; Müller-Schwarze 2009), and visual cues (Thorson, Morgan, Brown & Norman 1998). Perceived risk of predation also appears to affect diet choice: grey squirrels trade-off energy intake (Lima et al. 1985) and handling time (Lima & Valone 1986) against the risk of predation while foraging at a distance from safety, showing a preference for consuming smaller food items at the foraging patch, a behaviour which quickly increases energy consumption, while preferring to transport larger food items to the safety of cover for consumption.

Grey squirrels might also benefit from conspecifics while foraging at the same patch which might be an adaptation to lessen predation risk. While foraging alongside others, individuals have less chance of being detected and increased probability of escaping if they are attacked (‘dilution effect’), they do not need to visually scan for predators as frequently (‘many-eyes’ detection effect) so can spend less time being vigilant and more time feeding (Delm 1990; Bednekoff & Lima 1998). Furthermore, information detected about potential predation threats is likely to be of improved quality among a group, compared to that gathered by lone foragers (Bell, Radford, Rose, Wade & Ridley 2009). Research on group living species supports these “safety in numbers” hypotheses with studies reporting reduced vigilance with increasing group size (“the group size effect” reviewed by Roberts, 1996). Likewise, feeding rates decline among smaller groups, possibly owing to the increased need for vigilance: a meta-analysis by Verdolin (2006) reports that foraging success is reduced when individuals spend more time engaging in anti-predator vigilance. In grey squirrels, foraging effort is increased when there are conspecifics present: Hopewell et al. (2008) found that they increased their rate of returning to a nut patch, spending less time transporting items, when conspecifics were present compared to when foraging alone, and Bowers et al. (1993) report that they spend less time searching for food if there are fewer other foragers. These studies could indicate that the presence of conspecifics at a patch allows individual squirrels to engage in increased foraging because of the lessened predation risk. However, given that grey squirrels are not a group living species, these findings might also be explained by foraging competition, which will be considered next.

It has been theorized that although increased group size while foraging helps to lessen the risk of predation, the reason for reduced vigilance among larger foraging groups might not be directly linked to the safety of the group. The 'scramble competition' hypothesis suggests that vigilance declines as a function of increasing feeding rate due to greater competition for food while foraging among groups (Beauchamp 2003). As a result, there are costs for predator detection with less time devoted to being vigilant (Beauchamp & Ruxton 2003). A number of studies have investigated and modelled scramble competition with varying results. For instance, Beauchamp and Livoreil (1997) investigated the many eyes hypothesis in spice finches (*Lonchura punctulata*) and found that vigilance levels decreased with group size. However, they also found that foraging and feeding rate increased with group size, which is consistent with the view that vigilance is decreased owing to increased competition, as opposed to reduced predation. On the other hand, some studies have found more influence of predation risk than competition under group foraging competition (Lima, Zollner & Bednekoff 1999), and Bednekoff and Lima (2004) report that scramble competition only holds for stable small groups; individuals in larger groups feed considerably less because of the increased competition. Nevertheless, the relationship between these three factors is complex and multiplicative, with the effects of predation interacting with the effects of competition upon vigilance and feeding levels.

With regard to squirrel foraging behaviour, though the group size effect and scramble competition hypothesis have not been tested among grey squirrels, it is likely that due to the nature of their foraging both might be involved. A number of studies report that they trade-off foraging decisions based upon predation risk (e.g., Lima et al. 1985), and individuals are also highly competitive for resources yet still forage at the same patch as conspecifics, suggesting that this might be adaptive for predator avoidance. However, how foraging competition and predator vigilance are traded-off against one another to influence foraging strategy is unknown in grey squirrels. Whether there is also a trade-off implicated in caching decisions among scatter hoarders will next be addressed.

The effect of predation risk on caching decisions

From the previous discussion, it is evident that foraging animals face a complex trade-off in choosing when and where to forage between the costs and benefits of social foraging and the costs of predation. For animals that scatter hoard food matters are yet more complicated. Not only will the trade-off with predation risk affect decisions while they are searching for food to eat, it will also be relevant while they cache the food item, and when they come to recover the cache. We know from a number of studies that scatter hoarders transport food to locations where the probability of pilferage is reduced (e.g., Muñoz & Bonal 2011; Stapanian & Smith 1986). In addition, they adjust their food storing behaviour in ways that minimise predation risk (reviewed below). However both of these types of study typically only consider the trade-offs between the benefits of limiting pilferage or predation separately against the energetic costs of where to place caches. In reality, for wild-living individuals they are likely to be highly connected. The next section will firstly review research that has been carried out concerning caching decisions in relation to predation risk, and then will consider how these decisions are affected by risks associated with competition, including pilferage risk.

While many studies have investigated the effects of predation risks on foraging decisions across many species, including hoarders, fewer have investigated how predation risk might affect caching decisions among food storing animals. Predation risk is likely to have considerable impact upon individual caching choices, such as whether an item is consumed or cached, and when and where it is buried. Grey squirrels have been found to preferentially cache items that have a greater consumption time, as opposed to eating them, meaning that the individual spends less time on the ground eating exposed to predators (Jacobs 1992). When predation risk is at its lowest individuals make more caches and take more time to cache (Merriam's kangaroo rat: Leaver 2004). Predation risk might also influence decisions about where the item is stored, in terms of safety while caching and retrieving, in a similar way to how it affects where to forage versus where to eat (Lima et al. 1985).

Previous discussions have highlighted how many species of food hoarders are sensitive to pilferage risks while caching which can affect how, when and where they store food. However, the optimal conditions for minimising predation are frequently in conflict with ensuring security of caches. For instance, Daly et al. (1990) report that wider cache dispersion can increase predation risk due to increased exposure during travel time; but a number of studies show that caches that are dispersed more widely are also at lower risk of pilferage (Leaver 2004; Leaver et al. 2014; Male & Smulders 2007a; 2007b). Some species have been found to trade-off these risks while caching; studies show that various species of food hoarding animals prefer to space caches more widely if they contain favourable food items more than caches of less valuable foods (crested and willow tit: Jokinen & Suhonen 1995; Merriam's kangaroo rat: Leaver 2004; Leaver & Daly; yellow pine chipmunk: Vander Wall 1995; fox squirrel: Stapanian & Smith 1984; grey squirrel: Hadj-Chikh et al. 1996; red squirrel: Hurly & Robertson 1987; Steele, Hadj-Chikh & Hazeltine 1996; Longland & Clements 1995; Japanese squirrel, *Sciurus lis*: Tamura et al. 1999).

Few studies have directly investigated the trade-off between predation and pilferage risk among scatter hoarders, with those that have been conducted mainly measuring distance from cover as an assay of predation risk. These studies report that both artificial and natural caches placed in exposed locations are less likely to be stolen than those placed closer to areas that provide safety from predators, namely trees (artificial caches: Leaver et al. 2014; Steele et al. 2014; natural caches: fox squirrels: Stapanian & Smith 1986; Japanese squirrels: Tamura et al. 1999). Two field studies have directly compared the trade-off between pilferage risk and predation risk in food storing rodents. Leaver (2004) found that Merriam's kangaroo rat distributed favourable items more widely while caching despite the greater exposure to predators. Perea, González, San Miguel and Gil (2011) found that moonlight levels influenced pilferage of seeds in a nocturnal rodent, wood mouse, *Apodemus sylvaticus*. They found that seeds were removed more rapidly in open habitats and when there were increased moonlight levels, in comparison to sheltered locations. Grey squirrels have been reported to show a preference for caching in more exposed locations, as opposed to close to cover (fox squirrels: Stapanian & Smith 1986), or will cache more profitable food items in locations more exposed to predators than compared to non-profitable items (grey squirrels: Steele et al. 2014). Steele et al. (2014) suggest that caches closer to cover are more likely to be pilfered because there is lower risk of predation for opportunistic cache-pilferers to forage in these locations. Stapanian and Smith (1978; 1986) suggest that while cache-owners can move quickly and deliberately between their remembered caches in exposed areas, thieves must forage much more slowly in order to pilfer caches using olfactory cues, necessitating foraging in safer locations.

These studies illustrate that foraging individuals do not always act in ways to simply minimise predation risk, but that the role of the social environment heavily influences assessments of predation risk in relation to foraging and hoarding decisions. When making caching decisions, hoarders face a trade-off between minimising the risks of predation and reducing the risks that competitors pose to their caches; in terms of cache longevity, it can be more profitable to store food in areas of higher predation risk. Less is known about what specific cues individuals are responding to when making caching decisions based upon predation risks. It is evident that more research would clarify which aspects of social and predatory risks are responded to by grey squirrels and what contribution this makes to their foraging and caching decisions.

General conclusion

The body of this literature review has focussed upon the food storing and pilfering behaviour of corvids because more is known about how they respond to cache pilferage risk than in scatter hoarding mammals. The few field studies that have been conducted on grey squirrels indicate that they might share similar behaviour with corvids when making hoarding decisions. In terms of foraging and caching, controlled research is needed to investigate what specific cues squirrels are using to assess competition and pilferage risk. Individual differences are also thought to affect hoarding strategies in dominance-structured flocks of birds; given that research indicates that squirrels use dominance during foraging, it is possible that they might use it to form their caching decisions like in birds. Furthermore, heterospecific competitors might also affect foraging decisions in squirrels since they are known to compete for resources with different caching species, such as corvids. This literature review has also asked questions about cache pilferage from the perspective of the thief as well as the cacher; very few studies have investigated factors that influence pilfering success among scatter caching species. Because foraging and pilfering are not a simple one-way process for all hoarding animals, the questions addressed in this literature review have also highlighted how decisions about foraging competition and pilferage risk need to be considered from the point of view of a multi-way trade-off with predation risk, which bears the greatest fitness cost.

Thesis preview

As can be seen from the literature review, a wide range of studies have explored how corvids respond to different risks to their food hoarding behaviour. Fewer studies have investigated the behaviour of non-corvid scatter cachers in response to combinations of different risks upon foraging and hoarding. However, a handful of studies have indicated that wild grey squirrels might engage in similar behaviour to corvids in terms of the strategies they use to limit the costs of hoarding. This thesis presents two laboratory studies that have experimentally investigated how grey squirrels respond to different cues of pilferage risk (conspecific presence and cache loss), and whether conspecific audiences pose a risk to caching individuals. However, responding to pilferage risk is not a simple decision based upon the isolated cues that are presented in laboratory studies. Wild individuals face a multi-way trade-off in choosing where and when to forage, in terms of the costs and benefits of social foraging and the costs of predation. While elements of this trade-off have been considered before so that we know how grey squirrels respond to individual cues, the full system has not. Therefore, three field studies have been carried out that investigate different risk factors to foraging grey squirrels; in particular, how competition for resources, pilferage risk and predation risk interplay and affect food acquisition, storage and cache longevity. Note that it was in the nature of this research that several of the studies were conducted in parallel to one another. The laboratory studies were carried out consecutively but at the same time as the field studies. The locations of the field study presented in Chapters 5 and 6 did not overlap and therefore they were carried out at the same time as one another because they were examining behaviour that is seasonally based. The extent to which the different studies could build information on one another was therefore limited.

Previous studies carried out with grey squirrels in the field indicate that individuals are sensitive to the presence of conspecifics while storing food, and modify their future hoarding behaviour in response to experience of pilferage. In Chapter 2, results are presented from the first study conducted with grey squirrels that has manipulated both observer presence and pilferage experience while in a controlled laboratory environment. This study measured whether the subjects changed their eating and caching behaviour while under these conditions and whether they engaged in pilferage reduction behaviour that might serve to minimise the potential loss of their caches. This helps to clarify whether captive grey squirrels respond in a similar way to that seen in wild grey squirrels and laboratory studies conducted with corvids.

The fact that grey squirrels modify their caching behaviour while in the presence of conspecifics suggests that onlookers pose a threat to caches. A second laboratory study is presented in Chapter 3 which explored cache pilferage from the point of view of the pilfering squirrel. This study investigated whether grey squirrels have evolved the ability to use OSM to pilfer caches they have seen a conspecific make, a pilferage technique which has been reported in some species of corvid. In order to make direct comparisons with the few studies carried out with corvids an experimental set up that had already been used to test OSM was employed so that the results of the current study could be analysed in the same manner and more easily compared to existing studies.

Chapter 4 examines an alternative strategy by which squirrels might gain and maintain access to their resources (current, stored and stolen), namely social dominance. Some studies with other species of food hoarder indicate that dominant and subordinate individuals behave differently when storing food, with subordinate individuals being risk averse to predation cues to offset increased competition with more dominant individuals. This study has investigated this by measuring if social rank affected cache placement decisions relative to competition, pilferage and predation risks in a group of wild squirrels.

Chapter 5 further looks into the influence of decisions about predation risk but this time when pilfering caches. Previous research has indicated that there is a pilferage-predation risk trade-off when deciding upon the optimal place to store food, with items cached in locations high in predation risk associated with cache longevity. However, given that locations that provide cover and an escape route from predators, i.e., trees, also have abundant food availability, a higher density of competitors, and might act as beacons, it is difficult to conclude the contribution these other factors might be having on pilferage rates. This study experimentally investigated pilferage behaviour from the point of view of the thief in a natural setting. The pilferage rates of artificial caches were compared across four different types of visual cue that varied in whether they provided safety from predators, were a reliable food supply, or simply acted as a beacon. This provides insight into whether pilferers just target trees because they are beacons for caches or whether they target particular tress because they provide protection from predation risk and/or higher food availability.

In Chapter 6, a final study isolates responses to different risk factors to determine what contribution they make to foraging decisions. Different cues of risk were manipulated by presenting auditory playbacks to wild grey squirrels to simulate risks they might face while foraging: namely, risks posed by conspecifics and heterospecifics that compete for the same resources as squirrels, and risks posed by predators. Behaviour was monitored in response to the playbacks to determine the individual impact upon alert and foraging behaviours.

Finally Chapter 7 provides a general discussion and evaluation of the data chapters, and integrates what has been found from these new studies with what is currently known about Eastern grey squirrel behaviour.

Chapter 2: The effects of audience and pilferage on caching behaviour in the Eastern grey squirrel: a laboratory study.

Introduction

Food storing behaviour is widespread among birds and mammals that have evolved in an environment where the availability of food is variable according to season and individuals must compete for food resources. Animals hoard items such as nuts, seeds, and plant material, when supplies are abundant, and recover them during periods of low food availability (for discussions of the evolution of food hoarding see: Andersson & Krebs 1978; Roberts 1979; Smith & Reichman 1984; Vander Wall, 1990). However, these stores are vulnerable to theft by opportunistic foragers, with rates of pilferage estimated to be as much as 30% per day for some long term hoarders (Vander Wall & Jenkins 2003, though the upper range of this figure has been questioned owing to the fact that it is predominantly based on data from experimenter-made caches: Leaver et al. 2007). Hoarding animals have evolved a variety of strategies that help to minimise the loss of their food stores to pilferers. Larder hoarders reduce the risk of their food being stolen by bulk storing food items around their nest site which they aggressively defend from thieves, while scatter hoarders disperse single items in multiple caches across many different locations within their home range. Higher rates of cache theft have been reported when food is stored in view of other hoarders compared to when caching alone (e.g., Burnell & Tomback 1985; Carrascal & Moreno 1993; Sherry et al. 1982; Vander Wall 1990; Vander Wall & Smith 1987). Some species have been reported to be sensitive to eavesdroppers at the time of caching and will alter their behaviour in the presence of potential competitors in ways that might help to minimise cache theft (for reviews of social factors implicated in caching behaviour see: Brodin 2010; de Kort et al. 2006; Dally, Clayton et al. 2006; Grodzinski & Clayton 2010; Vander Wall & Smith 1987). The current study adds to this growing field of research by exploring how the social environment and experience of pilferage affect caching behaviour in the Eastern grey squirrel.

Audience effects on caching

A variety of wild and captive studies investigating ‘pilferage reduction behaviours’ have been conducted among food storing Passeriformes and Rodentia. These report that hoarders adopt different strategies when storing food in audience situations in contrast to storing alone, which may serve to minimise cache loss to onlookers (see Table 1). A large number of studies have reported that some species within the Corvidae and Paridae are particularly sensitive to the presence of conspecifics while they are hoarding, and will engage in a variety of different strategies to reduce pilferage of their caches. Some of these strategies have been claimed to involve quite complex cognition, such as awareness of an observer’s visual perspective (for a recent discussion of this topic see Grodzinski & Clayton 2010, and references therein). A series of laboratory studies by Clayton and colleagues with Western scrub jays have investigated these behaviours in depth. Typically these studies employ two adjacent cages, one containing a caching bird and the other containing an observing bird. The caching bird is given the opportunity to cache in two visually and spatially distinct locations, one that the observer has full visual access to and one that is made more visually obscure (e.g., by being at a greater distance from the observer; by having a barrier: Dally et al 2005b; by being in a more shaded location: Dally et al. 2004). The researchers compare the birds’ location preferences and the type of strategies used in the observed condition with when they cache in private. For example, Dally et al. (2005b) reported that, compared to when caching alone, jays caching in the presence of an observer preferred to hide items in distant sites and out-of-view and moved them multiple times while doing so; when the observer was removed they returned to their caches and re-cached them in a new location. Furthermore, experienced jays (those that had experience of being a thief themselves) were more likely to re-cache after being observed compared to birds that did not have experience of pilfering (Emery & Clayton 2001).

Table 1. *Different "pilferage reduction behaviour" documented among food hoarding birds and mammals when in audience conditions.*

Class	Strategy	Species
AVES: *Corvidae & Paridae*	Cache less in the presence of observers / more when alone	Clark's nutcracker: Clary & Kelly (2011); coal tit: Brotons 2000; black-capped chickadee: Stone & Baker (1989); Eurasian jay: Goodwin (1956); grey jay: Burnell & Tomback (1985); magpie: Clarkson et al. (1986); Northwestern crow: James & Verbeek (1984); rook: Simmons (1968); Western scrub jay: Dally et al. (2005a); willow tit: Alatalo & Carlson (1987); Lahti & Rytkonen (1996)
	Cache more in the presence of observers / less when alone	Eurasian jay: Bossema (1979); raven: Heinrich & Pepper (1998); Western scrub jay: Emery et al. (2004)
	Eat more in the presence of observers	Nuthatch: Carrascal & Moreno (1993); rook: Dally et al. (2008)
	Delay the onset of caching when in the presence of observers	Magpie: Clarkson et al. (1986); black-capped chickadee: Stone & Baker (1989)
	Limit visual information by storing food with less visual access to observers	Magpie: Clarkson et al. (1986); mountain chickadee: Pravosudov (2008); raven: Bugnyar & Heinrich 2005; Bugnyar & Kotrschal (2002); Heinrich & Pepper (1998); Western scrub-jay: Dally et al. (2004; 2005b)
	Limit auditory information about the location of caches by choosing a quieter caching substrate	Eurasian jay: Shaw & Clayton (2012b); Western scrub jay: Stulp, Emery, Verhulst & Clayton (2009)
	Move caches when in the presence of observer	Eurasian jay: Cramp & Perrins (1994); Goodwin (1956); raven: Bugnyar & Kotrschal (2002); Western scrub-jay: Dally et al. (2005a, 2005b)

	Move caches when the observer is absent	Clark’s nutcracker: Clary & Kelly (2011); Eurasian jay: Goodwin (1955); raven: Heinrich 1999; Western scrub-jay: Emery & Clayton 2001; Emery et al. (2004); Thom & Clayton (2013)
	Spacing caches farther away	Grey jay: Waite & Reeve (1995); magpie: Clarkson et al. (1986); marsh tit: Sherry et al. (1982); willow tit: Lahti, Koivula, Rytkonen, Mustonen & Welling (1998)
	Use aggressive behaviour to protect caches	Eurasian jay: Bossema (1979); Goodwin (1986); Wilmore (1977); rook: Goodwin (1986); Western scrub-jay: Dally et al. (2005a)
	Using misinformation: caching inedible items; leading conspecifics away from food caches; making empty caches	Raven: Bugnyar & Kotrschal (2004); Heinrich (1999); rook: Seed et al., personal observation in Dally, Clayton et al. (2006)
MAMMALIA: Rodentia	Cache less in the presence of observers / more when alone	Eastern grey squirrel: Leaver et al. (2007); rat: Denenberg (1952); Miller & Postman (1946)
	Cache more in the presence of observers / less when alone	Korean field mouse and Chinese white-bellied rats: Zhang et al. (2011); white-footed mouse: Sanchez & Reichman (1987)
	Eat more in the presence of observers	Eastern grey squirrel: Steele et al. (2008)
	Limit visual information by storing food with less visual access to observers	Eastern grey squirrel: Leaver et al. (2007); Steele et al. (2008)
	Make more interruptions to caching	‘Curtailed digging’ Eastern grey squirrel: Hopewell & Leaver (2008); ‘multiple caches’ Steele et al. (2008)

	Spend more time disguising caches	Eastern grey squirrel: Hopewell & Leaver (2008)
	Move caches when the observer is absent	Merriam's kangaroo rat: Jenkins & Peters (1992)
	Spacing caches away from the source or more widely dispersed	Pere David's rock squirrel, Korean field mouse, striped field mouse, Chinese white-bellied rat, and rat-like hamster: Huang et al. (2011); Eastern chipmunk: Clarke & Kramer (1994); Eastern grey squirrel: Leaver et al. (2007); Hopewell et al. (2008)
	Switch from majority scatter hoarding to larder hoarding	Pere David's rock squirrel: Lu & Zhang (2005); Korean field mouse: Zhang et al. (2011); Merriam's kangaroo rat: Preston & Jacobs (2001)
	Use aggressive behaviour to protect caches	Eastern chipmunk: Clarke & Kramer (1994); Eastern grey squirrel: Leaver et al. (unpublished data); Merriam's kangaroo rat: Preston & Jacobs (2001); Merriam's kangaroo rat: Daly, et al. (1992)
	Using misinformation: making empty caches	Eastern grey squirrel: Steele et al. (2008)

Less is known about pilferage reduction behaviour in mammalian cachers. There appears to be some evidence that they might use similar strategies to those used by corvids and parids, as well as using different strategies to avoid pilferage (in Table 1). Table 1 shows that grey squirrels demonstrate a range of behaviours that might serve to lessen pilferage risk. Among this literature are three field studies conducted by Leaver and colleagues (Hopewell & Leaver 2008; Hopewell et al. 2008; Leaver et al. 2007) on caching behaviour in a population of wild Eastern grey squirrels. In these studies the researchers monitored squirrels' natural caching behaviour and found that they were sensitive to the presence of conspecifics and would use 'evasive tactics' when caching to minimise pilferage of their hoards. In particular grey squirrels would: space their caches farther apart; orient their backs to other squirrels when burying nuts (Leaver et al. 2007); show more vigilance behaviour; delay the start of their caching after collecting a nut; spend more time disguising their caches with leaf litter, especially when caching a preferred hazelnut compared to a non-preferred almond; make more curtailed digs whereby the individual begins digging to deposit a food item but then interrupts the behaviour by being vigilant and moving to a new location without depositing the item, particularly when storing preferred food items (Hopewell & Leaver 2008); and transport food items and cache them at farther distances from the food source when there are competitors around, especially when food availability is low (Hopewell et al. 2008). These studies provide a vital comparison to the literature which is dominated by studies carried out with corvids (advised by Dally, Clayton et al. 2006), as well as a useful platform to further investigate by what mechanisms grey squirrels are protecting their food stores.

Pilferage effects on caching

Studies that investigate social influences on caching (such as those in Table 1) typically assume that pilferage risk is determined by the presence of observers at the time of caching. However, there may be other ways that food-storing animals determine the risk of pilferage. An important variable to examine in these types of study is how prior experience of pilferage may influence future caching behaviour, which is much more difficult to control and monitor in field studies. As can be seen in Table 2, fewer studies of this nature have been conducted, even with birds. Furthermore the general methodology appears to be more variable than methods used in studies investigating audience effects, which can make it more difficult to make between-species comparisons. For instance, Hampton and Sherry (1994) reported that black-capped chickadees will avoid caching in locations where they have had previous stores pilfered, and in a similar species Lucas and Zielinski (1998) found that Carolina chickadees cached more after experience of pilferage; while Baker and Anderson (1995) reported that the black-capped chickadees in their study did not adjust their behaviour in terms of caching location or quantity in response to pilferage. These differences could be due to inconsistencies in methodology. The birds studied by Baker and Anderson experienced complete pilferage, while those in the studies of Hampton and Sherry (1994) and Lucas and Zielinski (1998) only experienced partial loss of their food stores, as well as differing in whether the caching and pilferage was observed or not. Dally, Clayton et al (2006) suggest that partial pilferage encourages the expression of pilferage reduction behaviour, so that storers only engage in behaviour to protect their caches if there is some possibility that they could later recover at least some of them.

Table 2. *Different "pilferage reduction behaviour" documented among food hoarding birds and mammals after experiencing partial or complete pilferage.*

Class	Pilferage experienced	Strategy	Species
AVES: *Corvidae & Paridae*	Partial	Cache more	Carolina chickadee, *Poecile carolinensis*: Lucas & Zielmski (1998)
	Partial	Switch to caching a non-preferred item	Western scrub-jay: Clayton, Dally, Gilbert & Dickinson (2005)
	Partial	Move caches around more	Western scrub-jay: Dally et al. (2005a)
	Partial	Recover and eat more caches	Western scrub-jay: Emery et al. (2004)
	Partial	Reduce search times for caches, and decrease future caching, in pilfered locations	Black-capped chickadee: Hampton & Sherry (1994)
	Complete	Unaffected: do not avoid previously pilfered cache sites when storing food, and do not increase number of caches made	Black-capped chickadee, *Paws utricapihs*: Baker & Anderson (1995)

MAMMALIA: Rodentia	Partial	Cache in out of view sites	Eastern grey squirrel: Steele et al. (2008)
	Partial	Move caches to an non-preferred location	Merriam's kangaroo rat: Preston & Jacobs (2005)
	Complete	Increase scatter hoarding and decrease larder hoarding	Pere David's rock squirrel, Korean field mouse, striped field mouse, Chinese white-bellied rat, rat-like hamster: Huang et al. (2011)
	Almost complete pilferage	Increase larder hoarding and decrease scatter hoarding	Merriam's kangaroo rat: Preston & Jacobs (2001)
	Complete	Increase distance items buried from food source	Pere David's rock squirrel, Korean field mouse, striped field mouse, Chinese white-bellied rat, rat-like hamster: Huang et al. (2011)

Within the rodent literature Preston and Jacobs (2001, 2005) have directly compared the responses of Merriam's kangaroo rats to the mere presence of a competitor *versus* when competitor presence was paired with pilferage. They reported that kangaroo rats did not change their caching strategy in response to the mere presence of a conspecific (Preston & Jacobs 2001) or heterospecific (Preston & Jacobs 2005) competitor, but they did when presence of a competitor was also paired with pilferage. Preston and Jacobs suggest that kangaroo rats assess pilferage risk from experience of being pilfered and alter their future cache strategy to minimise further risk. The only study (to my knowledge) that has investigated the effect of cache loss on pilferage reduction behaviour in Eastern grey squirrels is that of Steele et al. (2008). In a series of field experiments with wild squirrels the researchers attempted to elicit different kinds of 'pilferage averting behaviour' by robbing caches. The researchers presented a series of nuts to a focal squirrel, and after several caches were made, another researcher removed the last cache that the squirrel had made while attempting to remain in the visual presence of that squirrel. Another series of nuts was then presented to the squirrel and its pilferage averting behaviour was monitored. They found that squirrels were more likely to cache nuts in “sites that were either out of view of or inaccessible to observers” (p. 711) following experience of pilferage. The researchers regarded this as evidence that squirrels engage in pilferage averting behaviour after witnessing partial pilferage of their caches by a human.

The field studies conducted by Leaver and colleagues and Steele et al indicate that squirrels might be responding to cues of pilferage risk (the presence of conspecifics) as well as observation of cache pilferage (albeit by a human) by changing their caching behaviour. However, unlike with the Passeriform literature, these claims have not been tested experimentally under controlled laboratory conditions, and so it is difficult to isolate the precise cue that squirrels use to assess pilferage risk while caching; whether, as in corvids, conspecific presence specifically cues responses to pilferage risk among grey squirrels, or if they respond more to pilferage itself, as in kangaroo rats. These factors have not previously been tested together, and therefore the aim of the current study is to investigate whether observer presence and / or experience of pilferage in a laboratory environment induces pilferage reduction behaviour in grey squirrels.

Audience and pilferage effects on caching

In the current study six captive squirrels were presented a pile of 15 intact hazelnuts and their behaviour was monitored under five experimental conditions: being observed by a squirrel, being observed by a human, being observed by a squirrel plus experiencing total pilferage of caches, being observed by a human plus total pilferage of caches, and being pilfered but not observed. Behaviours were compared to a baseline when the focal squirrel was not observed or pilfered. We measured whether the subjects changed their eating and caching behaviour (latency to cache, latency to eat, number of caches, number of nuts eaten) while under these conditions and whether they engaged in pilferage reduction behaviour that might serve to minimise the potential loss of their caches (caches recovered then reburied, caches recovered then eaten, curtailed digging, caching orientation, cache location). In light of the research that has been discussed, we predicted that subjects would respond to conspecific cues of pilferage risk and / or experience of pilferage by changing their future caching and eating behaviour and engaging in more pilferage reduction behaviour, but they should not respond to mere human presence as a source of pilferage risk because humans do not normally pose a risk to squirrel caches.

Method

Ethics and licensing

The study conformed to the Association of Animal Behaviour Guidelines for the Use of Animals in Research (2012), and was carried out with permission of the University of Exeter Psychology Ethics Committee. Subjects were housed at the University of Exeter, with permission of the Home Office because of restrictions in UK law for handling non-native species.

Animals

The subjects comprised six captive-raised Eastern grey squirrels (four males and two females) obtained from wildlife charities, unable to be re-released into the wild according to UK law (Wildlife and Countryside Act 1981). Five subjects were aged 1-2 years and one subject was aged 7-8 years old at the time of testing. Four of the subjects were housed in separate adjacent cages within the same room, and two of the subjects were housed together but in a separate room to the four other squirrels. The study took place during the spring and summer of 2011 and 2012 but not all squirrels were housed and tested at the same time. Subjects had not previously participated in cache-pilfering experiments.

Housing and apparatus

The housing and testing cages were the same as those reported in Hopewell, Leaver, Lea and Wills (2009) but with different furnishings in the testing cages. Housing comprised four large indoor cages: three cages were in the same room and were adjacent to one another (each cage size 1.9 x 1.8 x 2.5 m), and the fourth cage was in a separate room (size 3 x 1.8 x 2.5 m). Each cage was formed of metal mesh and concrete walls and equipped with various furnishings including shelves, nest boxes, cardboard tubes, shredded paper bedding, ropes, small branches, and wood shavings on the floor. These home cages were set to a 12L:12D light period and a temperature of 19°C. The subjects were fed each evening after trials had finished for that day. They were fed in their home cages on a mixture of flaked maize and wheat, dried vegetables and seeds, and a water bottle was available at all times filled with fresh water and dietary supplement (Vetzyme Stress®).

Attached to each of the three adjacent cages was a shared tunnel made of wire mesh which ran from the top of each cage to the testing room. The tunnel had a manually controlled metal plate door at the entrance to the test cage, and at the entrance to each of the squirrel’s cages. The tunnel was designed so that only one cage had access to a test cage at any one time. The tunnel of the single cage in the separate room had independent access to the test room through a hole in the cage wall (20 x 20 cm), manually operated by a plate door. Over a period of several weeks leading up to testing, subjects were trained to use this tunnel to access and cache in the testing room.

The subjects were tested in a separate testing cage to their home cage which was in an adjoining room to the two home cage rooms, and consisted of a large cage (3 x 1.8 x 2.5m) made of metal mesh and with concrete walls (see Figure 1). This cage was divided in half by a metal mesh wall, and each half of the cage could be accessed by the experimenter through a door on the front mesh wall. Both sides to the cage could be accessed by the squirrel through a small door (20 x 20 cm) in the central divide which the experimenter could control from outside the cage. The floor of the test cage was lined with ceramic tiles; six metal caching trays (each 30 x 5 x 30 cm) were placed on the floor in one of the test cages, and each tray was filled to the surface with wood shavings. During caching trials a pile of 15 in-shell hazelnuts were placed on the floor in the centre of the test cage; we chose in-shell hazelnuts as the focal food item because during prior food-preference testing these nuts appeared to be the cached items of choice, and they have been favoured in previous caching studies due to their energy content (Hopewell & Leaver 2008). Temperature was kept at a constant 19°C; lighting in the room was controlled by the experimenter and remained on at all times the subjects were in the test room. A water bottle was placed in both sides of the test room filled with fresh water and Vetzyme Stress® supplement.

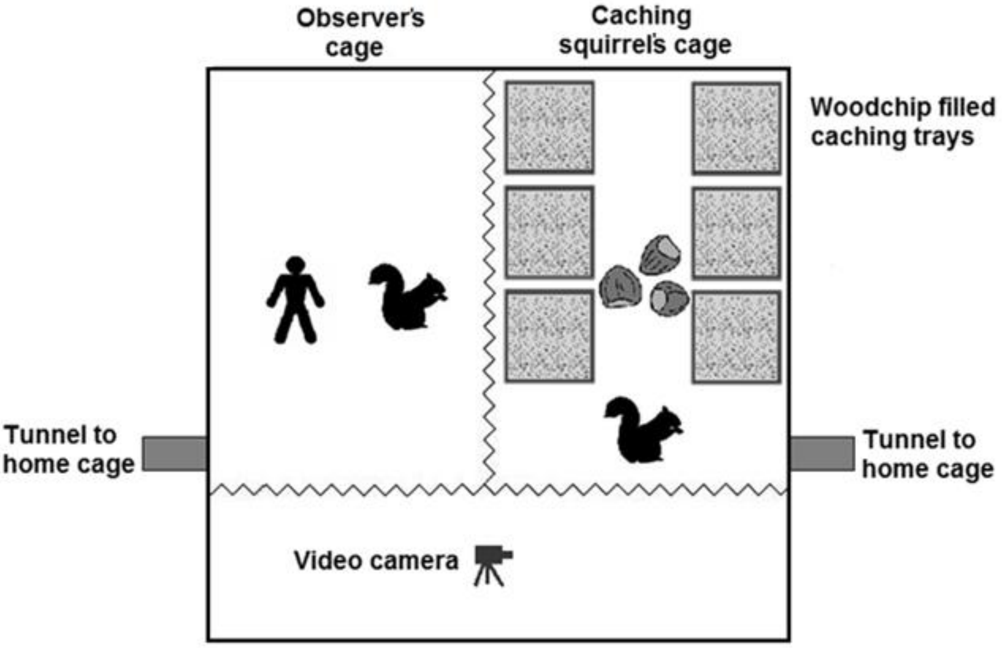


Figure 1. An example arrangement of the test room and test cages (not to scale). The caching trays were positioned so that there were three along the centre dividing wall and three along the opposite concrete wall. We adjusted which cage the caching trays appeared depending upon which home cage the subject squirrel was accessing the test room from.

During experimental trials behaviour of the focal subject was recorded using a hand-held video camera (Panasonic SDR-H90) positioned in a tripod 1m outside the focal squirrel's cage door; this allowed behaviour during the experimental trials to be viewed multiple times for accuracy. Within each of the home rooms and the test room, surveillance cameras were installed so that the squirrels could also be monitored remotely in live experiment through a PC outside the test room, using the software ViewCommander-NVR Version 4.

Experimental design and procedure

The experiment used a within-subjects design that consisted of alternating baseline and treatment blocks (presented in a randomised order for each subject) as shown in Tables 3 and 4. Each baseline and treatment block consisted of three repetitions of trials conducted on separate days (with the first repetition of each block acting as a learning trial). The experiment lasted a total of 33 non-continuous days of testing for five squirrels and 15 days of testing for one squirrel (who died before the study was completed), but in order to reduce possible boredom effects testing days were not run concurrently. The interval between trials within a block was 24-48 hours, and the gap between each condition was 48-72 hours. The experiment was completed in two sections for operational reasons: some squirrels showed a decreasing tendency to enter the test room over time, so this was combatted by introducing a lengthy rest period into the study for all of the squirrels; this also controlled for seasonal effects as subjects could be tested in the same time of year. Blocks 1-5/6 were completed first and then there was an approximate nine month interval before blocks 6/7-11 were completed. After each caching trial subjects were allowed to return later that day to recover their caches in private and determine their fate. All caching trials lasted approximately 60-90 minutes depending upon the following pre-determined criteria: the subject had been in the test cage for a minimum of 30 minutes, and since it had last eaten or cached there had been a period of inactivity for 15 minutes, at which time the trial was ended.

Table 3. *Description of the experimental conditions. Subjects were exposed to each of the treatments in a randomised order (but always commencing with baseline 1).*

Block	**Condition**	**Description**	**Duration**
1	Baseline 1	Unobserved and unpilfered.	1 learning + 2 experimental trials.
2	Treatment A	Caching in front of squirrel with no pilferage.	1 learning + 2 experimental trials.
3	Baseline 2	Unobserved and unpilfered.	1 learning + 2 experimental trials.
4	Treatment B	Caching in front of human with no pilferage.	1 learning + 2 experimental trials.
5	Baseline 3	Unobserved and unpilfered.	1 learning + 2 experimental trials.

6	Treatment C	Caching in front of squirrel with pilferage.	1 learning + 2 experimental trials.
7	Baseline 4	Unobserved and unpilfered.	1 learning + 2 experimental trials.
8	Treatment D	Caching in front of human with pilferage.	1 learning + 2 experimental trials.
9	Baseline 5	Unobserved and unpilfered.	1 learning + 2 experimental trials.
10	Treatment E	Unobserved and pilfered.	1 learning + 2 experimental trials.
11	Baseline 6	Unobserved and unpilfered.	1 learning + 2 experimental trials.

Table 4. *Order that each subject was exposed to each of the experimental conditions over the two testing periods of the study. During analysis one of the baselines blocks was randomly selected to act as a comparison control condition.*

Squirrel identity	**Treatment order for testing period 1**	**Treatment order for testing period 2**	**Control condition**
Arnold	C D	E B A	Baseline 4
Leonard	E A B	C D	Baseline 5
Perky	D C	-	Baseline 3
Sarah	B E A	D C	Baseline 6
Simon	D C	B A E	Baseline 2
Wonder	C D	A E B	Baseline 1

During baseline trials the subject was in the test room alone and was permitted to eat or cache items at will. The subject was allowed to return to its home cage and all remaining un-cached nuts were removed. Approximately 3 hours later the subject was allowed to return to the testing cage to recover its caches to eat or re-cache. The recovery trial lasted approximately 30 minutes. Caches remained in place for the duration of the baseline trials, but were removed at the end of each block.

During the treatments the subjects were observed caching by either another squirrel or by a human observer in the adjacent test cage. In the squirrel observer treatment the observer was a non-cage-mate and non-roommate squirrel. In the human observer treatment the observer was the principal experimenter (K.J.), however during the trial the experimenter was dressed in all-black clothing – at all other times the experimenter wore laboratory clothing around the subjects (white lab coat or white overalls). The human observer would sit on the floor in the centre of the observer cage, facing toward the testing cage, while remaining silent; when the focal squirrel moved position in the test cage, the observer would orientate their head toward their position in order to ensure their gaze was always fixed on the focal individual. When the subject returned for its recovery trial the caches had either been removed by the experimenter or were left intact, depending upon the condition. On trials where the caches were not removed they remained in place for the duration of the treatment trials, but were removed at the end of each block.

During the trials where the caches were pilfered, the principal experimenter removed all caches before the recovery trial. For the unobserved pilfered treatment the experimenter wore latex gloves to remove the caches. For the human observer condition the experimenter did not wear gloves while removing the caches and ensured that the scent from her hands was distributed throughout the substrate. For the squirrel observer condition the experimenter removed the nuts from the caching trays wearing latex gloves. Following this the squirrel that acted as the observer during that trial was allowed to access the test cage to explore the caching trays for 5-10 minutes so that they contained its scent cues.

Behavioural scoring

For each subject, one of the baseline blocks was selected randomly (using trials 2 & 3) to act as a comparison ‘unobserved unpilfered’ condition with which to compare the other 5 treatment conditions (see Table 4); this meant that all conditions would have the same number of testing days (note that there was little variability across the baseline trials between blocks, Appendix A). Behavioural measurements were manually scored from watching digital media files of video playbacks. We predefined behaviour using an ethogram (see Table 5) and measured the following: latency to cache, latency to eat, number of caches made, number of nuts eaten, number of caches recovered then reburied, number of nuts recovered then eaten, number of curtailed digs, orientation to neighbouring cage when caching, and location of caches in relation to neighbouring cage. During video scoring the principal experimenter was blind to all the conditions, except for the conditions which had an observing squirrel in the neighbouring cage (because the observing squirrel could frequently be seen).

Table 5. *Ethogram of behaviour coded from the videos during experimental and baseline trials.*

Strategy	**Behaviour**	**Description**
Eating versus caching preferences	Latency to cache	Caches were operationally defined according to the following description that has been adapted from Laidler (1980), Macdonald (1995), and Steele et al. (2008): The squirrel finds a nut, picks it up in its mouth, and manipulates it with its front paws. It then locomotes with the nut in its mouth, often making several stops and sniffing the ground. Sometimes the squirrel digs at the ground surface material with its front paws but then continues to move with the nut in its mouth, and may do this several times (**curtailed digging)**. Eventually the squirrel stops with the nut, while still holding it in its mouth, digs at the ground, and then deposits it into the freshly dug hole. The squirrel uses its front paws and nose to push the nut further into the site and uses several thrusts of its whole body. If the behaviour resulted in a nut buried, the time of the first thrust was the **latency to cache**. This distinctive thrusting action is usually only performed after they have deposited the nut (however, see Steele et al. 2008). Finally the squirrel covers the site with substrate and pats down the resulting cache with its front paws. When the squirrel leaves the location of the cache, it is clear that the squirrel is no longer carrying a nut in its mouth.

	Latency to eat	The subject makes an effort to break into a nut using its teeth (accompanied by a scratching sound) which was recorded as the *start time* of the behaviour; followed by consuming the contents of the nut. This does not simply involve manipulating a nut with its paws and teeth to change its orientation, and refers to intact hazelnuts only, not discarded shells or woodchip.
	Number of caches made	The number of *new* caches that have resulted from the trial. Does not include nuts dug up before the end of the trial.
	Number of nuts eaten	The number of nuts the squirrel broke open and consumed the contents.
Pilferage reduction behaviour	Number of caches recovered then reburied	An existing cache is dug up, held in mouth and front paws, and then re-buried according to the caching description above. The nut might have been re-buried at the place it was recovered, or moved and re-buried some time later.
	Number of nuts recovered then eaten	An existing cache is dug up and then consumed according to the eating description above.
	Number of curtailed digs	Also see the description of curtailed digging under the caching description above and Hopewell and Leaver (2008). The squirrel must have been holding a nut at the time of the dig. The behaviour does not immediately result in a cache.
	Orientation to neighbouring cage when caching	Orientation was recorded as either *facing* (consisting of a front or side view) or not facing (with back to) adjacent cage.
	Location of cache in relation to neighbouring cage	The precise location the cache was buried in was noted and recorded as either near or far to the adjacent cage.

Analysis

We used a 2 x 3 repeated measures design which examined the main effect of pilferage risk (pilferage, no pilferage), the main effect of observer presence (unobserved, human observer, squirrel observed), and an interaction between these two variables. Five subjects (*N* = 5) were tested across the six conditions, using the two consecutive experimental trials from each block, and one subject (*N* = 1) across three conditions (non-independent observations *n* = 10-12).

Generalised Estimating Equations (GEE) were used for most of the analyses in this study. GEE allows for analysis of related repeated measurements in non-normally distributed data (Ballinger 2008; Garson 2012; Hanley, Negassa, Edwardes & Forrester, 2003), accommodates for a small and uneven number of subjects by allowing all data points to be included in the sample size (Hanley, Negassa, Edwardes & Forrester 2003) and allows for a robust estimation of regression parameters and the production of standard errors (Ghisletta & Spini 2004). Furthermore, GEE allows for variable interactions to be investigated, which standard non-parametric analyses of correlated data do not allow for, thus providing the most comprehensive method of analysis for this data.

Separate tests were conducted to assess the main effects of condition on each of the dependent measures. GEEs were carried out using an inverse Gaussian regression (for positively skewed data without absolute zero values**)** with an identity link function (non-transformed) for latency to cache and latency to eat. GEEs were carried using a Tweedie regression (for a distribution with scale and absolute zero values) with an identity link function for number of caches made, number of nuts eaten, number of caches recovered then reburied, number of nuts recovered then eaten, and number of curtailed digs. All GEE analyses were carried out using a first-order autoregressive (AR(1)) working correlation matrix (for related measurements), and using pairwise comparison contrast tests with a Bonferonni adjustment for multiple comparisons. We report the best model based on the Goodness of Fit statistic quasi-likelihood under independence criterion (QIC) and the corrected quasi-likelihood under independence model (QICC, a corrected version that rewards parsimony), with smaller values indicating a better fit.

For analyses that where the GEE model was not appropriate or if data were normally distributed we used a repeated measures analysis of variance (ANOVA) examining the main effects of pilferage risk, observer presence, and an interaction between these two variables. To examine orientation to adjacent cage when caching we compared the proportion of caches made per trial when facing toward the adjacent cage with the proportion of caches made facing away from the adjacent cage, For caching distance to adjacent cage we compared the proportion of caches made near to the adjacent cage with the proportion of caches made far away from the adjacent cage). All reported data conform to assumptions of ANOVA (with equality of covariance matrices at a significance level above .001, and equality of error variances above .05, as defined by Pallant 2007), the more conservative lower bound epsilon value has been reported for sphericity, and Pillai's trace has been reported as it is a more robust multivariate test statistic (which accounts for small sample size and unequal *N* values: Pallant 2007).

Data were analysed using Microsoft Office Excel 2010 and SPSS 16.0 for Windows. Significant models are reported to minimum of 5% alpha level.

Results

Boxplots for all measures within the category *eating-caching preferences* and within the category of *pilferage reduction behaviour* are presented in Figure 2.

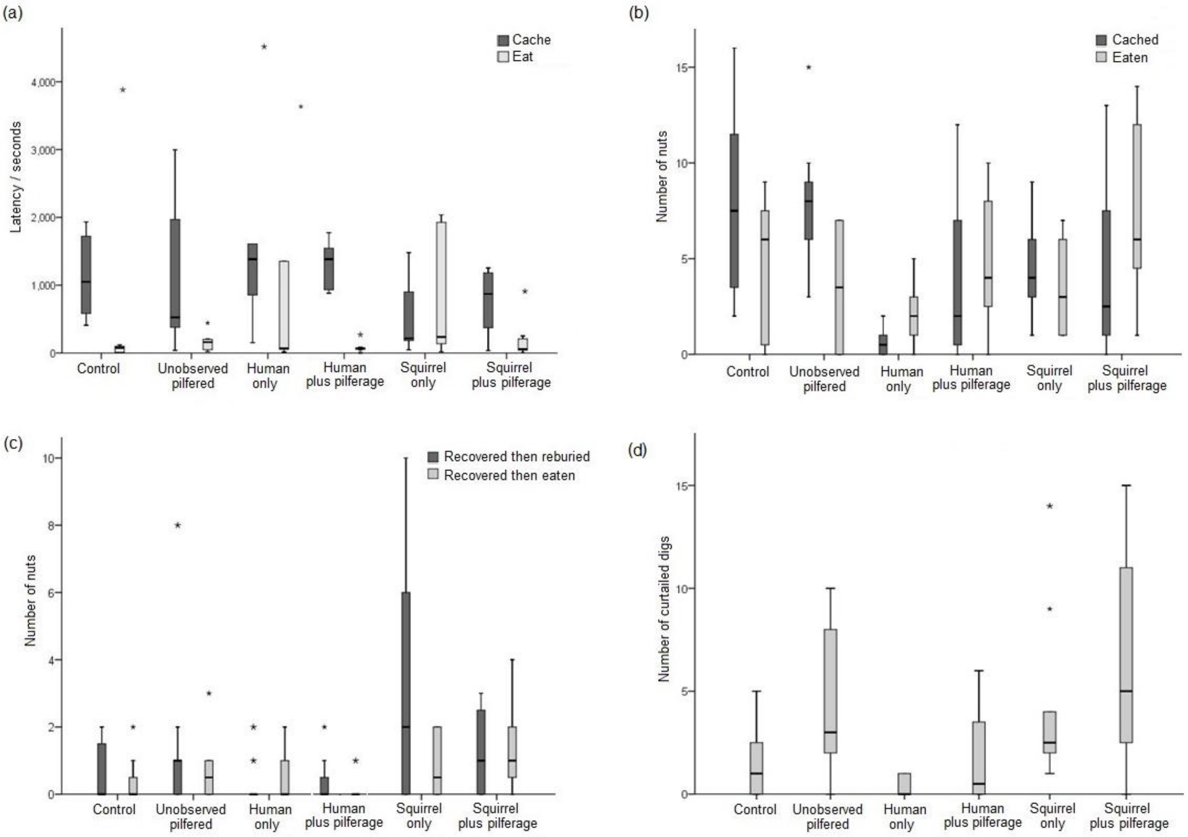


Figure 2. Boxplots comparing (a) the latency to eat and cache, (b) the number of nuts eaten and cached, (c) the number of nuts recovered then reburied or eaten, and (d) the number of curtailed digs made across each condition.

Eating versus caching preferences

A GEE was carried out for latency to cache which reported QIC = 2.131, QICC = 12.17. There was no main effect of pilferage (approaching significance, p = .052), there was a significant main effect of being observed, X^2 (df = 2, N = 6, n = 12) = 41.29, p < .001, and there was no pilfered x observed interaction (p = .169). The main effect of being observed is displayed in Figure 3 with results from follow-up pairwise comparison contrast tests which show that subjects cached significantly earlier when being observed by another squirrel compared to a human or when caching alone.

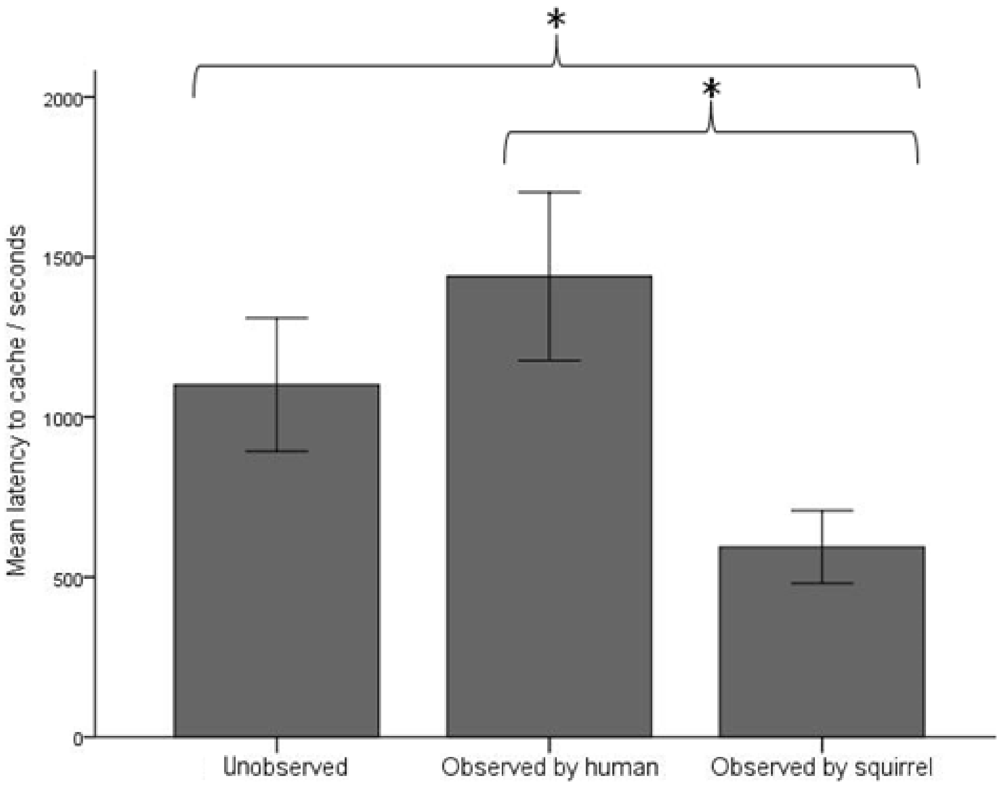


Figure 3 The effect of being observed on mean latency to cache. Bars represent ± 1 standard error. * *p* < .05.

A GEE was carried out for latency to eat which reported QIC = 4.411, QICC = 13.67. There was a significant main effect of pilferage, X^2 (*df* = 1, *N* = 6, *n* = 12) = 4.56, *p* = .033, there was no main effect of being observed (approaching significance, *p* = .096), and there was no pilfered x observed interaction (approaching significance, *p* = .099). Figure 4 shows that subjects started eating significantly earlier after experiencing pilferage compared to when they had not experienced pilferage.

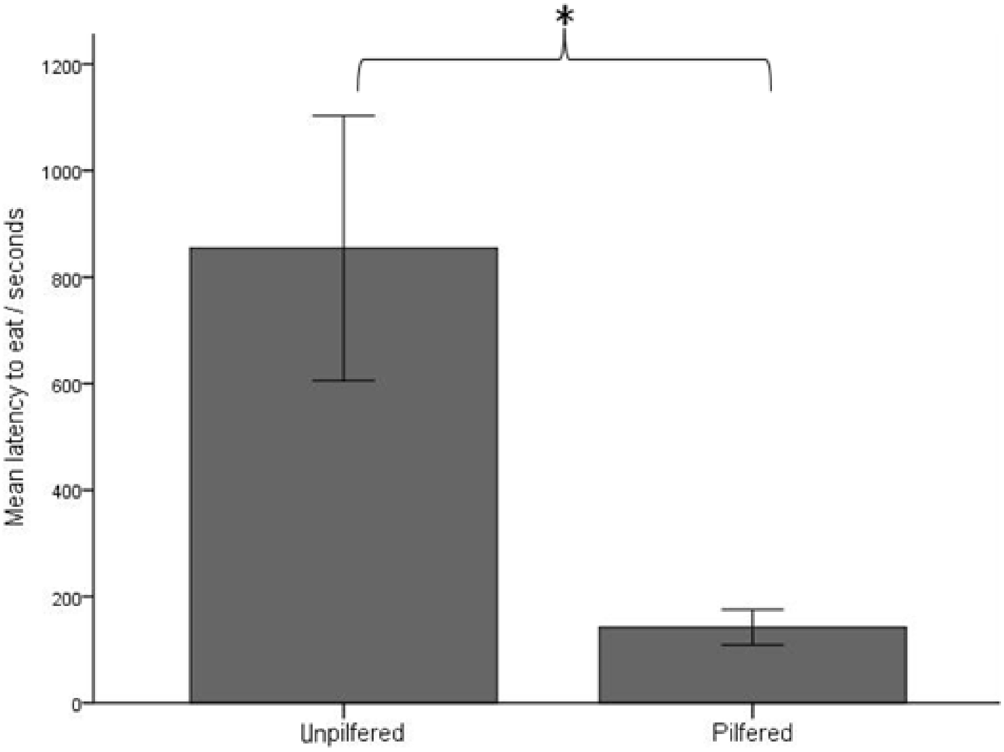


Figure 4 The effect of being pilfered on mean latency to eat. Bars represent ± 1 standard error. * $p < .05$.

A GEE was carried out for number of caches made which reported QIC = 132.83, QICC = 132.25. There was no main effect of pilferage ($p = .136$), the main effect of being observed was significant, X^2 ($df = 2$, $N = 6$, $n = 12$) = 113.45, $p < .001$, and there was a significant pilfered x observed interaction, X^2 ($df = 2$, $N = 6$, $n = 12$) = 10.55, $p = .005$. The main effect of being observed is displayed in Figure 5(a) with results from follow-up pairwise comparison contrast tests which show that subjects made fewer caches when being observed by another squirrel compared to when there was no observer, and even fewer caches when being observed by a human compared to not being observed. The pilferage x observer interaction is displayed in Figure 5(b) which shows that subjects cached less in all of the observed conditions compared to the unobserved conditions, and the fewest number of nuts when being observed by a human with no pilferage; thus not being pilfered resulted in fewer caches being made but only when being observed by a human.

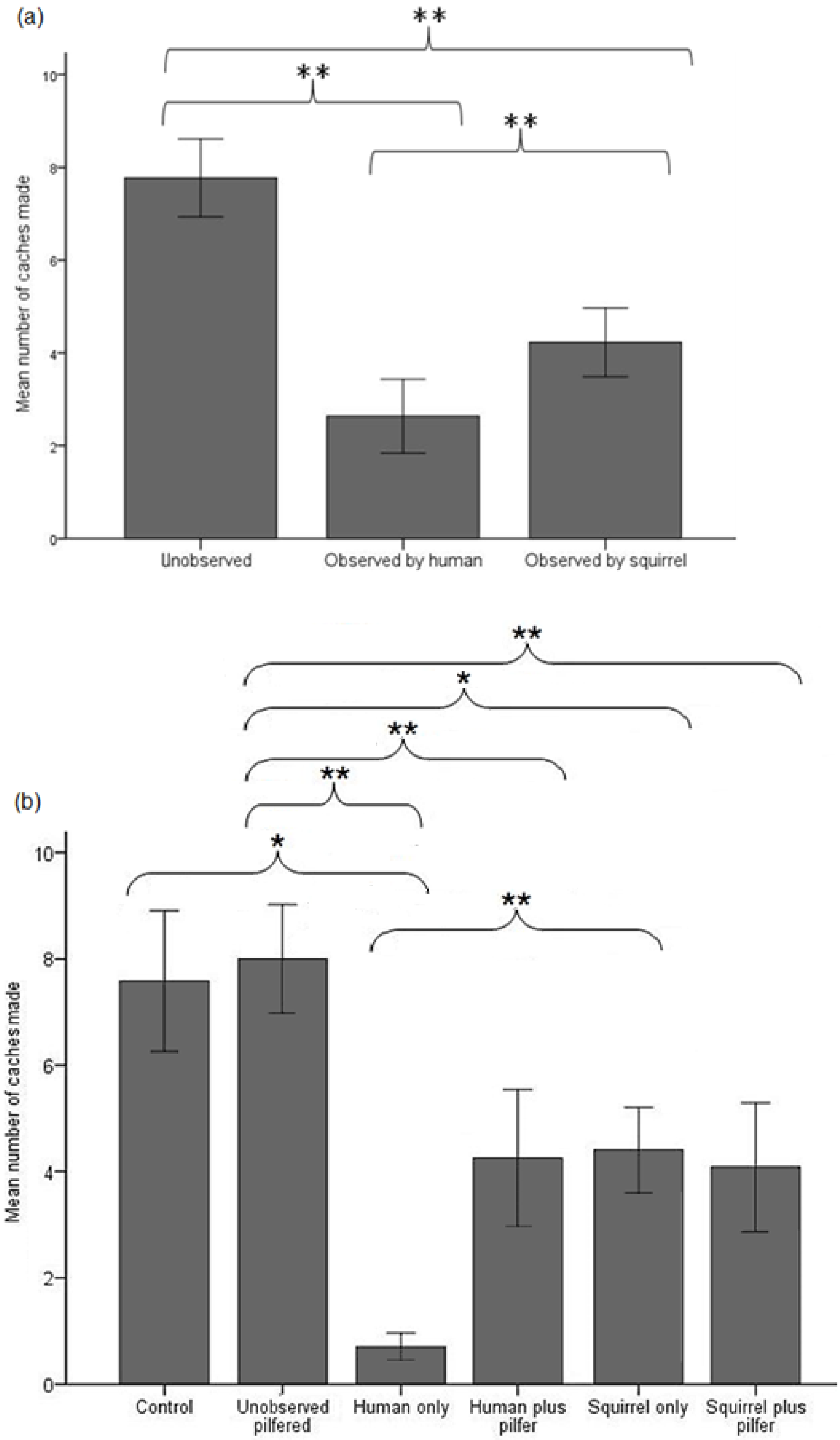


Figure 5. (a) The effect of observer presence and (b) pilferage paired with observer presence on the mean number of caches made. Bars represent ± 1 standard error. * *p* < .05, ** *p* < .001.

A GEE was carried out for number of nuts eaten which reported QIC = 127.86, QICC = 125.92. There was a significant main effect of pilferage, X^2 (df = 2, N = 6, n = 12) = 11.48, p = .001, a significant main effect of being observed, X^2 (df = 2, N = 6, n = 12) = 16.01, $p < .001$, and no pilferage x observed interaction (p = .130). The main effect of pilferage is displayed in Figure 6(a) which shows that subjects eat more following pilferage. The main effect of being observed is displayed in Figure 6(b) with results from follow-up pairwise comparison contrast tests which show that subjects eat more when being observed by another squirrel.

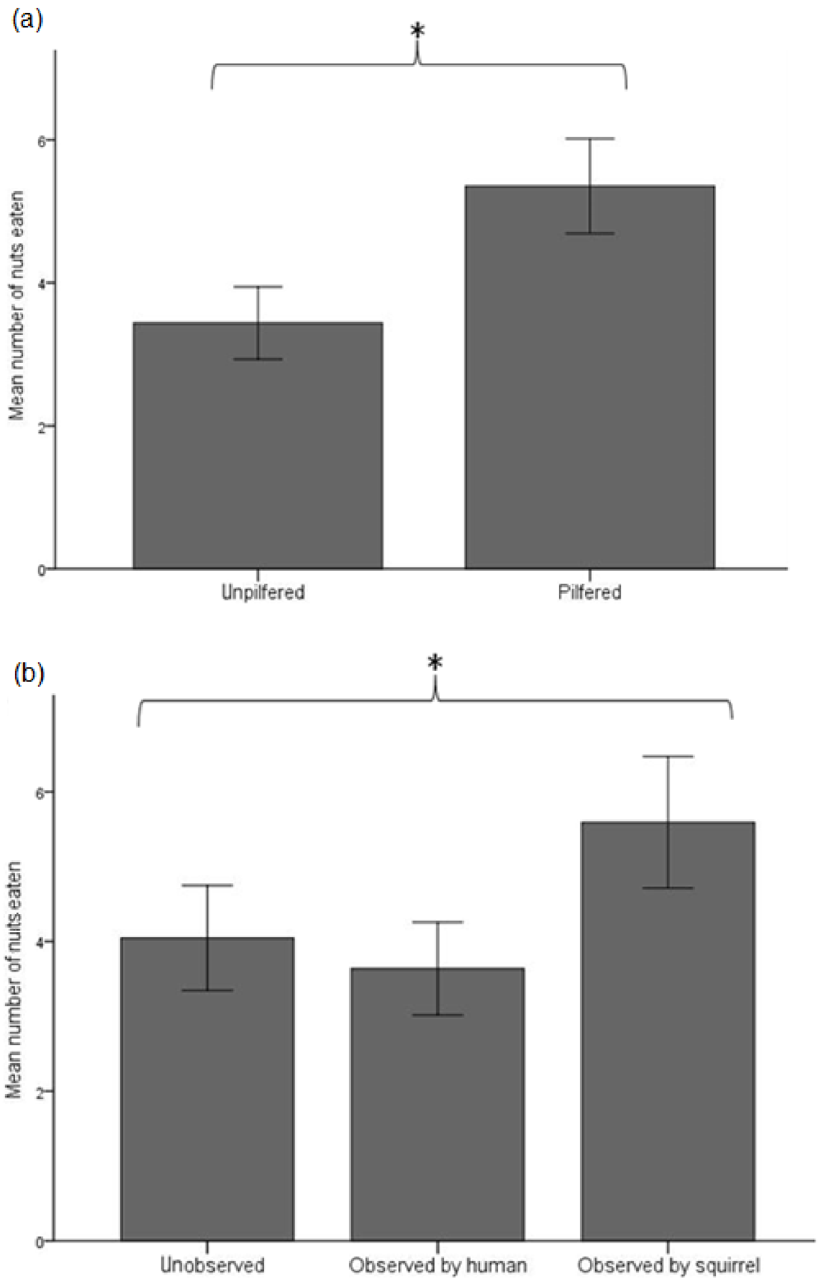


Figure 6. (a) The effect of being pilfered and (b) the effect of observer presence on the number of nuts eaten. Bars represent ± 1 standard error. * $p < .05$.

A GEE was carried out for number of caches recovered and then reburied which reported QIC = 252.16, QICC = 240.87. There was no main effect of pilferage (p = .467), there was a significant main effect of being observed, X^2 (df = 2, N = 6, n = 12) = 15.272, p < .001, and there was no pilfered x observed interaction (p = .378). The main effect of being observed is displayed in Figure 7 with results from follow-up pairwise comparison contrast tests which show that subjects re-cached more nuts when being observed by another squirrel.

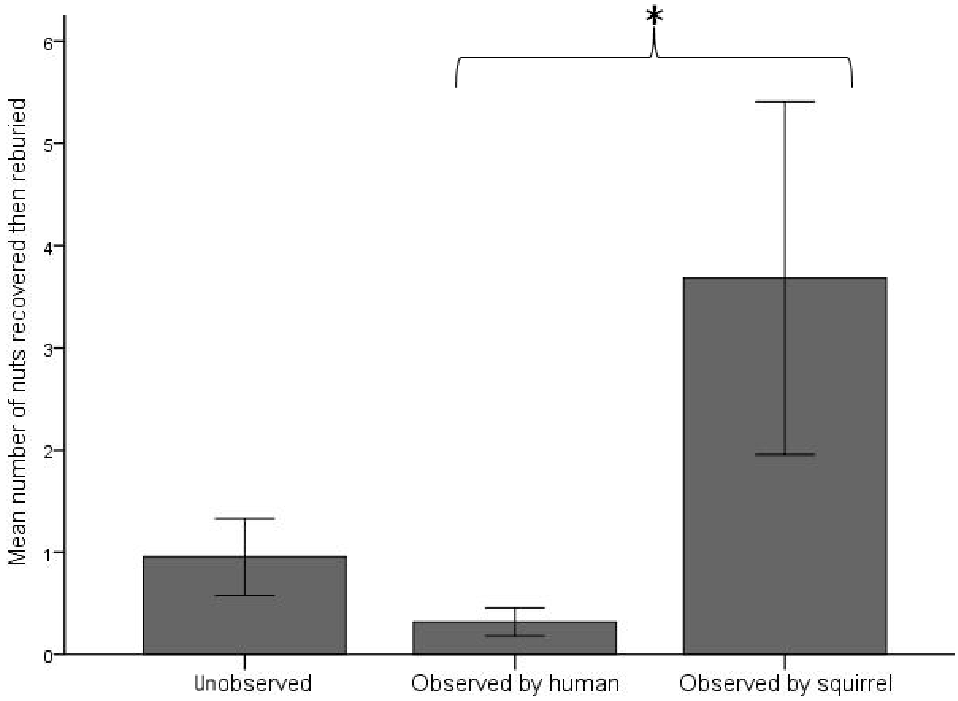


Figure 7. Effect of observer presence on number of caches recovered then reburied. Bars represent ± 1 standard error. * p < .05.

A GEE was carried out for number of caches recovered and then eaten which reported QIC = 138.35, QICC = 144.22. There was no main effect of pilferage (approaching significance, p = .074), there was a significant main effect of being observed, X^2 (df = 2, N = 6, n = 12) = 21.18, p < .001, and there no pilfered x observed interaction (p = .242). The main effect of being observed is displayed in Figure 8 with results from follow-up pairwise comparison contrast tests which show that subjects recover more caches to eat when being observed by another squirrel, and recover the least caches to eat when being observed by a human.

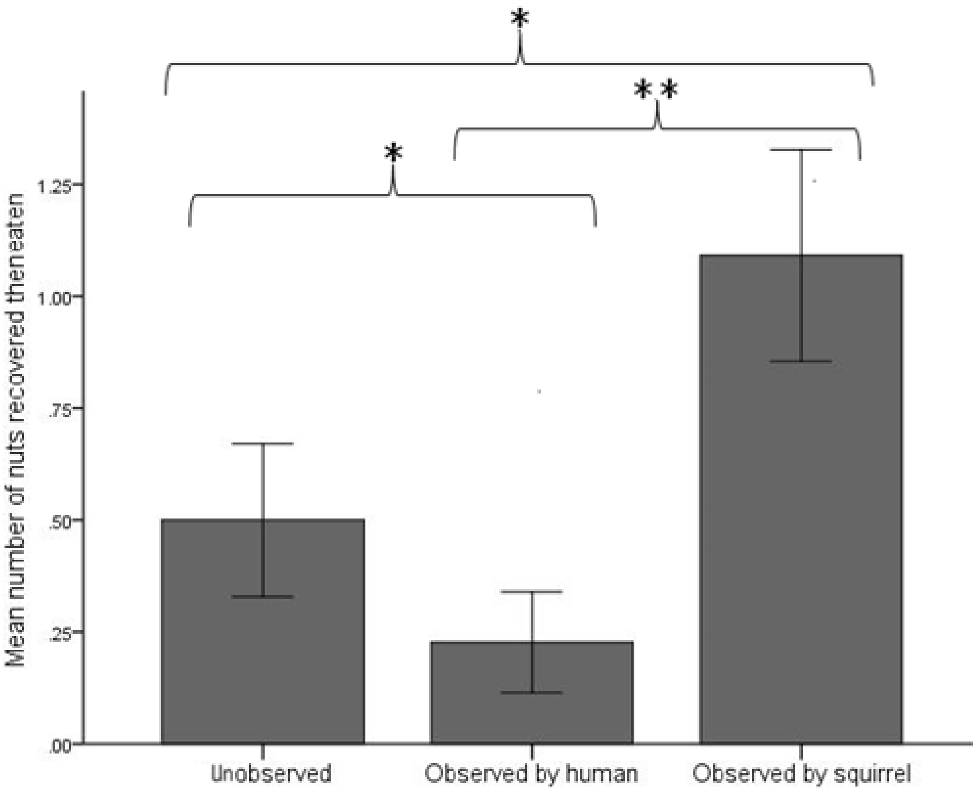


Figure 8. Effect of observer presence on number of caches recovered then eaten. Bars represent ± 1 standard error. * $p < .05$, ** $p < .001$.

A GEE was carried out for the number of curtailed digs made prior to caching which reported QIC = 181.85, QICC = 182.63. There was a significant main effect of pilferage, X^2 (*df* = 1, *N* = 6, *n* = 12) = 5.73, *p* = .017, there was a significant main effect of being observed, X^2 (*df* = 2, *N* = 6, *n* = 12) = 17.92, *p* < .001 and there was no pilfered x observed interaction (*p* = .368). The main effect of pilferage is displayed in Figure 9(a) which shows that subjects make more curtailed digs after experiencing pilferage of their caches. The main effect of being observed is displayed in Figure 9(b) with results from follow-up pairwise comparison contrast tests which show that subjects make more curtailed digs when being observed by another squirrel compared to a human observer.

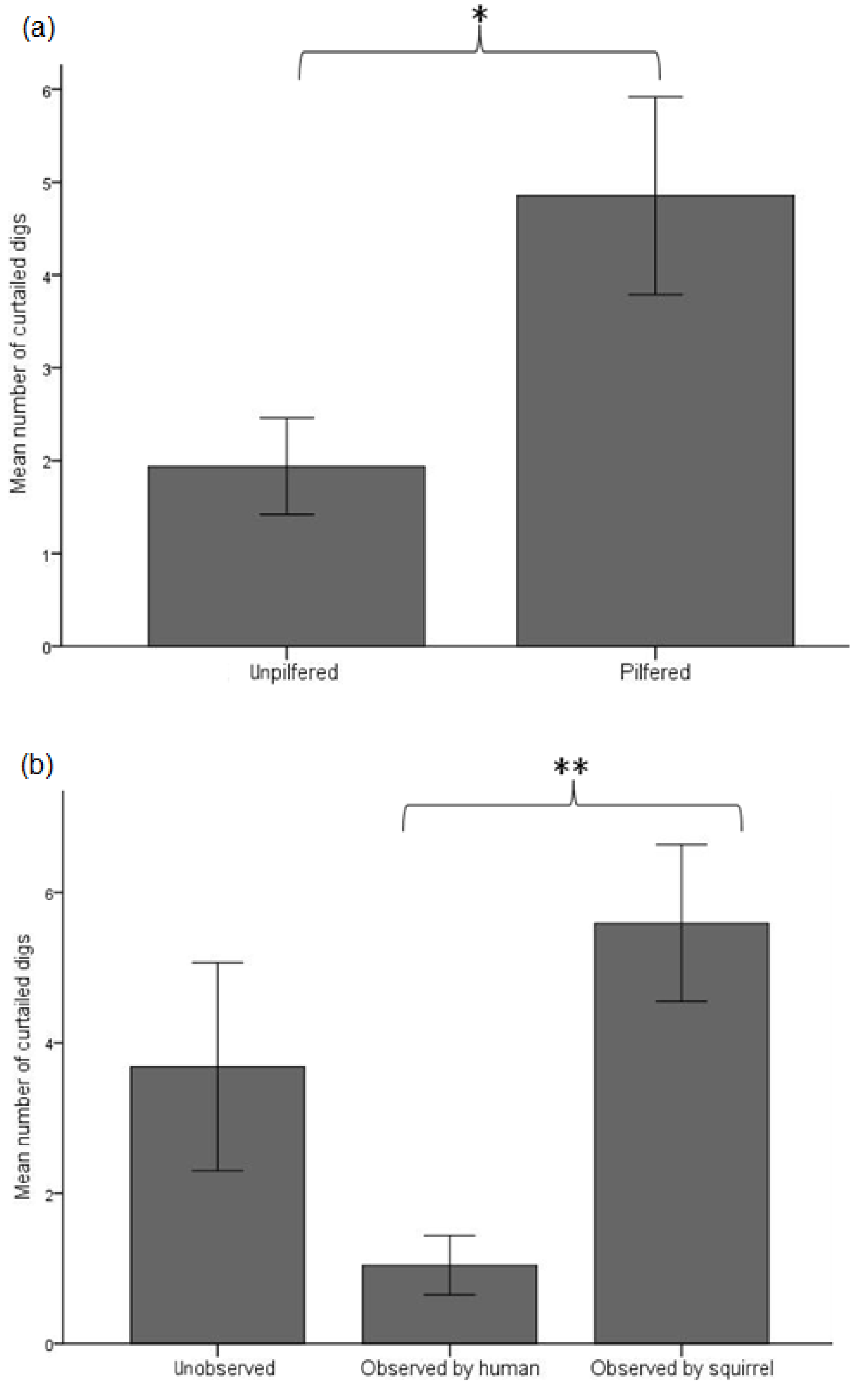


Figure 9. (a) The effect of being pilfered and (b) observer presence on the number of curtailed digs made. Bars represent ± 1 standard error. * $p < .05$, ** $p < .001$.

A repeated measures ANOVA was carried out to compare the proportion of caches buried near or far to the adjacent observer’s cage. There was no main effect of pilferage (p = .577), no main effect of being observed (p = .713), and no pilferage x observer interaction (p = .755).

A repeated measures ANOVA was carried out to compare the proportion of caches buried facing towards or away from the adjacent observer’s cage. There was no main effect of pilferage (p = .704), no main effect of being observed (p = .671), and no pilferage x observer interaction (p = .492).

Discussion

This study provides evidence that grey squirrels directly responded to both conspecific presence and pilferage experience and that they use this information when making caching decisions to avoid pilferage. Subjects were found to change their caching behaviour in response to being observed by a conspecific by caching earlier and making fewer caches, while their eating behaviour changed in response to pilferage experience with subjects consuming more nuts more quickly after caches had been pilfered. Being observed by a conspecific also resulted in more occurrences of pilferage reduction behaviour, including re-caching, eating caches and making more curtailed digs, while being pilfered also increased the number of curtailed digs made. Given that they responded similarly to being pilfered as being observed this indicates that pilferage reduction behaviour might come about because squirrels are uncertain about their caching decisions, as opposed to pilferage reduction behaviour serving a deceptive function. Being observed by a human seemed to have an inhibitory effect upon behaviour with fewer caches made and commencing later than compared to a conspecific observer, fewer curtailed digs, and fewer nuts recovered. Overall it appears that risk of pilferage posed by conspecific presence impacted on behaviour in ways that might serve to directly minimise future cache loss (making fewer overall caches, spending more time finding a suitable cache location, and moving and eating caches), whilst actual loss of caches encouraged more rapid consumption of available food.

Audience and pilferage effects upon caching decisions

This study provides strong support for the field studies of Leaver and colleagues that squirrels are sensitive to conspecifics as potential pilferers of their caches and actively engage in pilferage reduction behaviour, and also lends support to the work of Steele et al in that they also respond to experience of pilferage. Like kangaroo rats, grey squirrels do not live in groups (Koprowski 1996); observer effects are more commonly found in group-living species such as the corvids, that have a high occurrence of observing other flock members cache. However, this study shows that squirrels respond in similar ways to corvids to safeguard their caches, as well as assessing prior pilferage risk as reported in kangaroo rats. Furthermore, these behavioural strategies appear to be ecologically adaptive. When caches are at risk of future pilferage it is adaptive to invest more time in securing these long term energy reserves by minimising the possibility that nearby observers can locate caches; spending more time caching and re-caching, consuming caches, and making curtailed digs can serve to confuse onlookers to the whereabouts of buried food (Hopewell & Leaver 2008; Steele et al 2008), or even obscure olfactory cues. However, in circumstances where caches have already disappeared it is more adaptive to make use of immediate energy reserves if more pilferage will occur (discussed in Sherry 1985, but also see Lucas, Pravosudov & Zielinski 2001). This appears to be a similar strategy to that reported in some of the corvid literature; for instance, Emery et al. (2004) reported that scrub jays switched their caching and recovery behaviour after being pilfered from predominantly re-caching to predominantly eating the contents of caches. Emery et al. suggest that this flexible caching strategy is advantageous because eating these items when the risk of theft is high enables them to generate internal energy reserves.

Our results show no effects of observer presence or pilferage experience on caching orientation and location. Field studies of grey squirrels also report similar behaviour: Leaver et al. (2007) report that squirrels orient their backs to other squirrels when burying, and Steele et al (2008) found that they will hide food in out of view locations after experiencing pilferage. Within the corvid literature researchers have found that captive birds are highly sensitive to these factors; as well as being responsive to the mere presence of onlookers (because it cues pilferage risk), they also appear to be aware of the observer's visual perspective and choose to cache in locations that are more visually obscure to their onlookers (e.g., Dally et al. 2005a; 2005b; Dally et al. 2004). The current findings could be explained by the experimental set-up of the study which constrained cache placement to a much smaller area than that of wild squirrels, particularly so the caching squirrel was never out of visual contact with the observer. It would be informative to conduct further controlled studies in a similar vein to those of Clayton and colleagues (e.g., including visual barriers) to further investigate what specific factors of the social environment influence these caching decisions; specifically whether grey squirrels are simply using a rule-of-thumb to assess pilferage risk based on observer presence or whether they are sensitive to the observer's viewpoint at the time of caching, like corvids (e.g., Dally et al. 2004; Dally et al. 2005).

We also found that squirrels made even fewer caches and recovered and ate fewer nuts when they were being observed by a human, compared to when being observed by another squirrel. The squirrels in this study were fully habituated to, and did not appear fearful in any way of, human presence. However, there is a possibility that even human-raised squirrels have an innate tendency to be weary of humans. Very little research has investigated foraging and caching decisions in relation to human presence. Leaver et al. (2014) found that wild squirrels did not adjust their distance to the safety of cover in response to changes in human disturbance levels when caching or foraging; unlike the research of Steele et al. (2008), this supports our current data that squirrels do not view human presence a source of pilferage risk. An alternative reason for our current findings could be because human presence might represent a different cue to these captive squirrels, namely a source of food. It would therefore not be adaptive to engage in energetic costly behaviour such as burying and recovering caches when humans represent a usually predictable source of food. We do not know whether a wild population of squirrels would demonstrate similar behaviour; frequently wild squirrels do approach humans for food, at least in urban environments. It is however, extremely unlikely that wild or captive squirrels would normally regard humans as a source of competition for resources or caches.

Studying laboratory housed squirrels

There are always limitations in studies of this nature, which is true of most behavioural research conducted in laboratory environments. For a species that scatter hoards across their entire home range area, captive testing arenas cannot represent natural caching behaviour on an ecologically realistic scale (Hitchcock & Sherry 1995). This may account for some of the findings already discussed (caching orientation and location). Perhaps more naturalistic captive settings (such as wildlife sanctuaries that cannot re-release their grey squirrels, and can house them in very large outdoor enclosures) would be a more favourable setting to carry out future studies of this nature. It is also difficult to gain large enough sample sizes in captive studies, particularly when rearing and housing non-domesticated species that are not particularly suited to such environments. Nevertheless, even with a small sample size, the results from the current study reveal some important behavioural data that provide a platform from which future research can be carried out.

As well as future studies manipulating the influence of the observer as outlined above (e.g., by incorporating visual barriers in this type of study design), it would also be interesting to vary pilferage experience. Some studies selectively ‘pilfer’ certain caches rather than removing them all (Hampton & Sherry 1994) to see if the subjects learn which areas are more risky for caching. As pilfering does not suppress caching completely it might be interesting to investigate if repeated partial pilfering at the same locations affects decisions about where future caches are buried. Indeed, partial theft of caches would provide a more ecologically relevant model of cache robbing, and could be investigated with wild marked subjects.

Conclusion

We conclude that scatter hoarding mammals can respond directly to conspecific presence as a cue of pilferage risk and also to experience of pilferage. We have shown that they will flexibly adjust behavioural strategies in ways that may help in preventing future cache pilferage. Similar controlled studies could identify the mechanisms involved in these behaviours in order to facilitate further understanding of what squirrels know about their observers and whether perhaps more complex cognition is involved, as reported in corvids.

Chapter 3: The role of observational spatial learning in cache pilfering by Eastern grey squirrels: a laboratory study.

Introduction

For food hoarding to be an evolutionary stable strategy a cacher must have a recovery advantage of its own stores (Andersson & Krebs 1978; for an alternative view see Smulders 1998; Vander Wall & Jenkins 2003), storing food in such a way that others are prevented from stealing it while the cacher is able to successfully recover it (Kamil & Balda 1990). The literature reviewed in Chapter 2 illustrates the risks that cachers face in securing their stores, and reveals some of the ways different species go about minimising these risks. For example, individuals are sensitive to audiences while caching and will minimise opportunities for their caching behaviour to be observed by others. Such behaviour would be adaptive if onlookers are able to locate a cache through observation; that is, to commit its location to spatial memory and recover that information at a later time. We know that spatial memory plays an important role in the behaviour of many scatter hoarding birds and some scatter hoarding mammals (including grey squirrels) in recovering their own food stores (reviewed in Smulders et al. 2010). However, some species of food storing corvid have been found to learn and remember the locations of caches that they have seen others make and use this information to pilfer stores when the cacher is absent. For an onlooker to successfully pilfer by observation, the individual must possess highly accurate observational spatial memory (OSM). The current study aims to investigate whether grey squirrels have evolved a similar ability to use OSM to pilfer caches; an ability that we would predict to find, given their careful and extensive behavioural adjustments during caching when in the presence of conspecific observers, several of which appear to conceal information of the whereabouts of their caches (reviewed and experimentally tested in Chapter 2).

Pilfering behaviour

Pilfering the food caches of others offers an individual access to resources without having the time and energetic costs associated with foraging and caching (Shaw & Clayton 2012b). Despite the large number of studies on food caching across different species, information on the behaviour of pilferers is limited. When recovering their own caches, individuals are reported to use a number of different strategies: olfactory information (deer mouse: Vander Wall 2000; grey squirrel: Calahane 1942; Jacobs & Liman 1991), visual cues (reviewed in Chapter 5) and spatial memory (corvids, parids and rodents reviewed in Smulders et al. 2010). There is evidence that they might use some of these strategies when recovering artificial caches or pilfering the caches of others: random olfactory search (Clark's nutcracker: Kamil & Balda 1985; deer mouse: Howard & Cole 1967; Howard et al. 1968; VanderWall 2000; grey squirrel: McQuade et al. 1986; magpie: Buitron & Nuechterlein 1985; Merriam's kangaroo rat: Reichman & Oberstein 1977; raven: Harriman & Berger 1986; yellow pine chipmunk: Vander Wall 1991) and visual cues (reviewed and experimentally tested in Chapter 5). However, very few studies have investigated whether OSM might be used to pilfer caches that an individual has observed being made.

Pilferage can occur under two circumstances: immediately after a cache has been observed, or after a delay. A number of caching species have been observed to pilfer by observation immediately after they have witnessed a cache made, allowing them immediate access to the energy store of another individual, with minimal energy expenditure from foraging. However this does carry the risk of the cache owner still being nearby which could result in an agonistic encounter. The safer option is to remember the spatial location of the cache and return to pilfer it after some time has elapsed. By using OSM to pilfer caches there are a number of benefits over other pilferage strategies. A pilferer can visit a cache site after a storer is no longer present, thus avoiding potential conflict arising from cache defence (Emery 2004). Remembering the locations of others caches means that less time is spent foraging or searching for stores through random search and so reduces energy expenditure. OSM allows the thief to locate a cache quickly and accurately, minimising exposure time to potential predators and interaction with competitors (Bednekoff & Balda 1996a).

OSM in caching birds and rodents

There are no field studies that have experimentally tested and found OSM in scatter hoarders, owing to it being difficult to study in wild populations. The few laboratory studies that have been carried out tend to involve small numbers of captive birds, particularly corvids. Typically these studies involve a caching bird and an observer bird placed in two adjacent cages. The observing bird watches the caching bird bury several food items; the caching bird is removed, and the observer is given access to the caching arena after varying time intervals. Studies have found that some food storing corvids can accurately recover caches they observed being buried by another cacher, but the delay after which accuracy declines varies between species. It has even been reported that the pilferers frequently engage in behaviour that facilitates observation of caching behaviour, such as changing their position and orientating themselves to gain a better view of a caching conspecific (raven: Bugnyar & Kotrschal 2002; Eurasian jay: Shaw & Clayton 2012b; Thom & Clayton 2013; Western scrub jay: Grodzinski, Watanabe & Clayton 2012). A list of the species that OSM has been studied in and whether OSM has been demonstrated is presented in Table 6.

Table 6. *Studies that have investigated or reported OSM among different caching species*.

Species	**Dependency upon caching**	**Evidence of OSM**
Corvidae		
Common magpie	Moderate generalist cacher, makes short term stores throughout the year (Clarkson et al. 1986; de Kort & Clayton 2006).	They have been observed following squirrels and stealing their caches after they have made them but it has not been experimentally tested whether they can do this after a time delay (Vernelli 2013).

Clark's nutcracker	Specialised cacher, shows seasonal peak in caching and is dependent upon long-term stores (Bednekoff & Balda 1996b; Vander Wall & Balda 1977).	Observers were found to perform at better than chance when recovering a cache they had seen a conspecific make after one day's delay only, though after two days cachers were more accurate than observers (Bednekoff & Balda 1996b).
Gray jay	Specialised cacher, shows seasonal peak in caching and is dependent upon long-term stores (Wait & Reeve 1992 in de Kort & Clayton 2006).	In a laboratory study jays did not accurately recover caches observed made by another bird after a few minutes' delay (Bunch & Tomback 1986).
Jackdaw	Infrequent cacher (Henty 1975; de Kort & Clayton 2006).	Compared to chance, observers do not accurately recover items after a 1 minute delay having watched these being buried by a human (Schied & Bugnyar 2008).
Mexican jay	Occasional cacher, not highly dependent upon stores (Bednekoff & Balda 1996b).	Observers perform as well as cachers at a delay of one and two days (Bednekoff & Balda 1996b).
Pinyon jay	Specialised cacher, shows seasonal peak in caching and is dependent upon long-term stores (Bednekoff & Balda 1996a)	Observers recovered caches better than chance after 1-2 days delay, but cachers made significantly fewer errors than observers (Bednekoff & Balda 1996a).
Raven	Moderate generalist cacher, makes short term stores throughout the year (Heinrich & Pepper 1998)	Observers can accurately pilfer the caches of conspecifics after a 5 minute interval (Bugnyar & Kotrschal 2002), they fail to recover caches they had not seen being made (Heinrich & Pepper 1998) and will recover items they observed buried by a human after a 1 minute delay (Schied & Bugnyar 2008).

Western scrub jay	Moderate generalist cacher, makes short term stores throughout the year (de Kort & Clayton 2006)	They will recover more food they observed being cached compared to when they did not observe the caching event after 4 hours (Griffiths et al. unpublished data in Clayton et al. 2001), they show a preference for watching caching-related behaviour in conspecifics compared to any other behaviour (Grodzinski, Watanabe & Clayton 2012), and they demonstrate mental rotation when pilfering caches they observed made by a conspecific (Watanabe & Clayton 2007).
Other species		
Black-capped chickadee	Specialised cacher, shows seasonal peak in caching and is dependent upon long-term stores (Sherry 1984).	In laboratory experiments observers will pilfer caches immediately they have observed made by another bird, but have a low recovery rate for caches when tested several hours later compared to their own caches (Baker et al. 1988; Hitchcock & Sherry 1995).
Eastern grey squirrel	Specialised cacher, shows seasonal peak in caching and is dependent upon long-term stores.	They have been observed watching cachers from tree-tops and then moving to the ground to pilfer, but it has not been experimentally tested whether they can do this after an extended delay (Steele et al. 2014).
Great tit	Non-hoarder	In the laboratory, great tits remembered the locations of caches made by marsh tits after a 1 hour and 24 hour interval (Brodin & Urhan 2014).
Merriam's kangaroo rat	Generalised cacher, dependent upon long-term stores (Leaver & Daly 2001; Seferta 1998).	There is only one anecdotal observation of caches being pilfered immediately after the cache was created (Daly et al. 1992).

North Island robin	Occasional short-term cacher, not highly dependent upon stores (Armstrong et al. 2012).	Observers can recover small numbers of items over short intervals (~1minute) that they observed buried by a human (Armstrong et al. 2012).

It has been suggested that species that perform well in OSM tests also tend to be social and rely heavily upon caches; in comparison those that perform less well tend to be not particularly social species (e.g., Clark's nutcracker: Bednekoff & Balda 1996b), or not highly dependent upon cached food (e.g., jackdaw: Schied & Bugnyar 2008). However, one study that investigated the use of OSM by a non-hoarding parid, the great tit, disputes this claim: in the laboratory great tits were found to remember the locations of caches made by marsh tits for up to 24 hours (Brodin & Urhan 2014). Thus it is possible that OSM might even be common to non-caching species that evolved alongside hoarders. Nevertheless, this is difficult to generalise because no other studies have investigated the use of OSM in cache pilfering within taxonomic groups other than corvids, such as rodents.

Pilfering and cache protection behaviour have been reported in a variety of food hoarding species, with many cachers engaging in behaviour that serves to limit the opportunity for onlookers to witness a cache. For this behaviour to be adaptive for the caching individual, the pilferer should benefit from observing a cache. In addition, many of these species also possess accurate spatial memory to locate their own caches. Therefore, it is likely that OSM might be more widespread among caching species than those that have been studied.

Bugnyar & Kotrschal (2002) suggest that the cachers and pilferers are engaged in an 'evolutionary arms race', where cachers develop methods to minimise the risk of cache pilferage, while pilferers develop strategies that allow them to more easily locate and steal others caches. Experimentally investigating whether non-corvid species possess OSM will help to determine how scatter hoarders actually engage in pilfering, and whether the so-called cache protection behaviours they perform serve a similar function to that suggested in corvids. This might help researchers in this field to understand whether similar adaptive pressures have led to the evolution of OSM among different caching species.

Grey squirrels and OSM

Grey squirrels present an ideal opportunity to study OSM in a mammalian species. In terms of their social system they are tolerant of conspecifics but actively compete with them for resources: they are predominantly non-social (Koprowski 1996) yet are non-territorial with overlapping home-ranges so many have access to the same food patch and will forage alongside one another (Lewis 1980; Vander Wall & Jenkins, 2003). Tree dwelling species of squirrel rely heavily on their visual system in comparison to other rodents (Van Hooser & Nelson 2006); grey squirrels have a wide visual field (Kaas et al. 1972), excellent spatial acuity (Jacobs et al. 1982), use spatial memory to recover their own caches, and use visual cues when recovering artificial caches (McQuade et al. 1986), all of which would facilitate pilfering by observation. Moreover, grey squirrels engage in behaviours that help to minimise the loss of their caches to pilferers; in the presence of conspecifics they will delay the onset of caching (experimentally reported in Chapter 2), cache less (Leaver et al. 2007; experimentally reported in Chapter 2), eat more (Steele et al. 2008; experimentally reported in Chapter 2), recover more caches (experimentally reported in Chapter 2) make more interruptions to caching (Hopewell & Leaver 2008; Steele et al. 2008; experimentally reported in Chapter 2), spend more time disguising caches (Hopewell & Leaver 2008), orientate away from observers (Leaver et al. 2007), store food in locations with less visual access to observers, and make empty caches (Steele et al. 2008). Ultimately, as suggested by Leaver et al. (2007), the fact that grey squirrels alter their caching behaviour in the presence of conspecifics suggests that onlookers pose a threat to caches. With these behavioural and morphological characteristics in mind, squirrels would benefit from possessing OSM to increase their pilfering success.

In order to be able to make direct comparisons of OSM abilities between species we adapted the experimental set up and procedures of our current study from Griffiths et al. (unpublished data in Clayton et al. 2001) and the training- and blind-test-trials of Watanabe and Clayton (2007), but without the more advanced rotation tests those authors used to test mental rotation ability. Employing an experimental set up that had already been used to test OSM meant that the results of the current study could be analysed in the same manner and more easily compared to existing studies.

During habituation trials we allowed laboratory housed grey squirrels to observe a conspecific cache and then after a fixed delay of watching the caching event the subject was given access to pilfer the caches with both visual and olfactory cues present. After the learning phase we then compared pilferage behaviour under two experimental conditions: (1) observers were prevented from watching the caching squirrel (but could still hear them) and caches remained intact, meaning that they could only use odour cues to locate the caches; (2) observers witnessed caching but the caches and odour cues were removed before pilfering was allowed, meaning that observers could only use visual information to locate the (empty) cache sites. The efficiency and accuracy of search and pilferage behaviour (and pilferage attempts when caches were removed) was recorded. We predicted that if OSM was being used by squirrels to locate caches then they would be more accurate and efficient in their searching and pilfering behaviour after they had witnessed the caches being made compared to when they had not seen them being made but could only rely on olfactory cues.

Method

Ethics and licensing

The study conformed to the Association of Animal Behaviour Guidelines for the Use of Animals in Research (2012), and was carried out with permission of the University of Exeter Psychology Ethics Committee. Subjects were housed at the University of Exeter, with permission of the Home Office because of restrictions in UK law for handling non-native species.

Animals

The subjects comprised four captive-raised Eastern grey squirrels (three males and one female: Arnold, Leonard, Simon and Sarah) obtained from wildlife charities, unable to be re-released into the wild according to UK law (Wildlife and Countryside Act 1981). At the time of testing three subjects were aged 2-3 years and one subject was 8-9 years old. Two of the subjects were housed in separate adjacent cages within the same room, and two of the subjects were housed together but in a separate room to the other squirrels. The study took place from February through April 2013 with trials run sequentially. Subjects had participated in one caching experiment approximately one year prior to this study, in which they experienced having their caches pilfered (presented in Chapter 2).One week prior to commencing the current study the subjects were familiarised with the new arrangement of the testing arena, where each squirrel was allowed to explore the apparatus for a few minutes each day leading up to their first day of testing, though during this time there was never any food available to cache in the test room. This meant that the first few days of testing were not affected by the subjects' experience of a novel testing environment.

Housing and apparatus

Housing conditions were the same as those described in Chapter 2, and the same testing room and cages were used but with different apparatus. Along the dividing mesh wall in each test cage was a curtain that could be rolled out on either side when needed to fully obstruct visual access between both sides of the cage. During the study one side of the testing cage acted as the *observer's cage*, while the other side acted as the *cacher's* cage. Eight metal caching trays (each 30 x 5 x 30 cm) were placed on the floor in one side of the test cage in a 2 x 8 formation along the central mesh wall. Each tray was separated into four sections by a wooden divider inserted into the tray, so that there was a total of 32 equal cells (15 x 15 x 5 cm), and each cell was filled to a 4cm depth with wood shavings (see Figure 10). Each subject had its own caching trays and sawdust that were re-used between trials; sawdust was mixed among cells between trays before each the start of each trial, and any soiled sawdust was removed in order to minimise odour cues within subjects. The experimenter wore latex gloves during handling of all material.

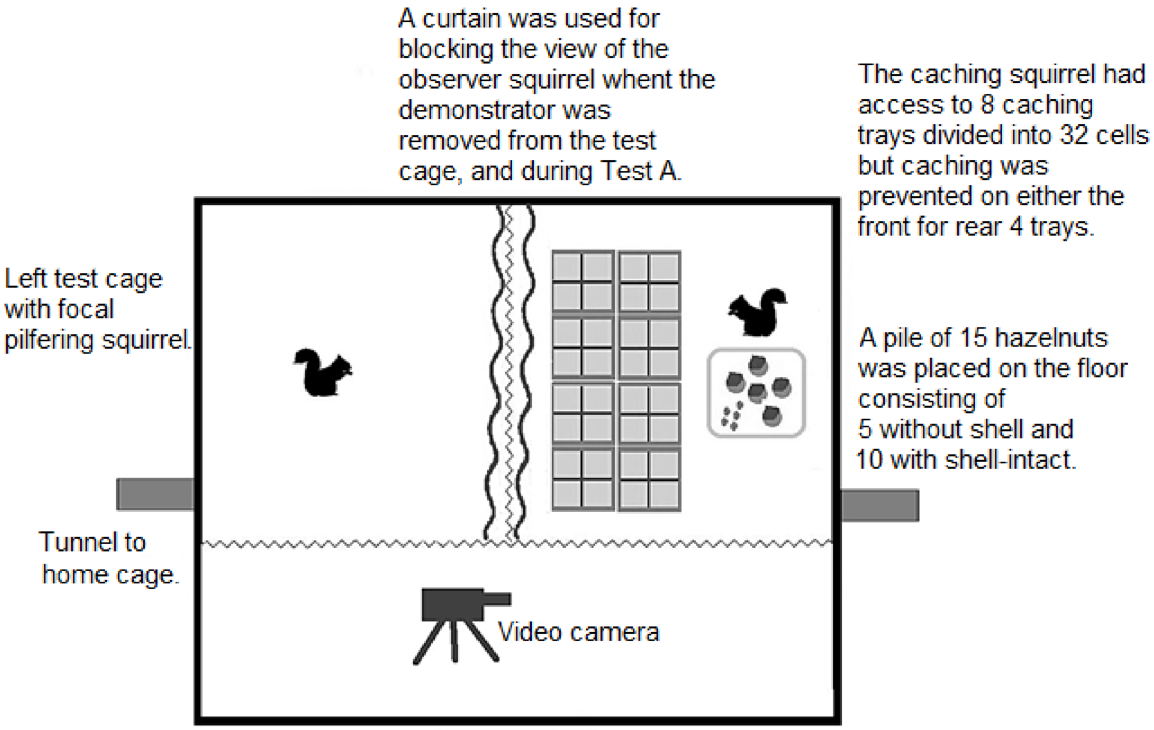


Figure 10. An example arrangement of the test room and test cages (not to scale). The caching trays were positioned along the centre dividing wall. We counterbalanced the placement of the caching trays between the two cages . When caching trays were on the left side of the test cage the arrangement was mirrored.

For each caching trial half of the sawdust-filled cells were covered using transparent laminate sheets that prevented caching in either the 16 front or 16 rear area cells of the cage. The location of the laminate covers alternated between trials for each subject and was counterbalanced across trials, repetitions and squirrels, which prevented the cacher from using the same locations throughout the experiment. Sixteen pieces of laminate covered the tops of the sawdust of each cell and were held in place using a Bulldog Clip ® along each side of the cell. Clips were also placed in the same position on the cells that did not have a laminate cover. A thin layer of sawdust was placed on the surface of each laminate to conceal any visual cues of its presence (e.g., reflection from room lighting). Between each trial the laminate sheets were cleaned with unscented anti-bacterial wipes and re-used.

During caching trials a pile of 5 hazelnuts without shells and 10 hazelnuts with shells intact were placed on the floor in the centre of the test cage. We used hazelnuts because they were found to be a cached item of choice compared to other intact nuts (discussed in Chapter 2). We also offered hazelnuts without shells because in a prior study the subjects frequently chose to eat several nuts before caching; offering hazelnuts with no shells meant that the trial could be run more quickly if the squirrel chose to eat items before caching (this procedure was also used by Watanabe & Clayton 2007 using a combination of live/dead wax worms, peanuts and husked sunflower seeds). At no time did a squirrel ever cache a nut that was not in a shell.

All observations were recorded using a hand-held video camera (Panasonic SDR-H90) positioned on a tripod 1m outside the focal squirrel's test cage door; this allowed observations to be conducted remotely and behaviour to be viewed multiple times for accuracy. Within each of the home rooms and the test room, surveillance cameras were installed so that the squirrels could also be monitored remotely in live experiment through a PC outside the test room, using the software ViewCommander-NVR Version 4. This meant that we could monitor experimental progress remotely without disturbing the subjects with our presence.

Experimental design and procedures

We used a within subjects design where all four subjects participated as both an observer and cacher, though our principal interest was the pilfering behaviour of the observer squirrel. For each observing squirrel, the experiment consisted of four trials (2 habituation trials followed by 2 test trials) where one trial was run every four days over a total 13 day period. During the four day break between trials, each subject acted as a cacher for another squirrel to observe but using the opposite side of the test cage so that their caching trays were absent, marking the trial as unique, and the laminate placed in the opposite location. After completing all four trials the subject had a seven day rest period before participating in a second repetition of the experiment. A total of three repetitions of the experiment were run which meant that each squirrel acted as an observer three times and as cacher to each of the other three subjects once.

Trials consisted of two habituation trials (differing in the location of the laminate covers), which were followed by two different test trials, A and B (differing in whether the observer squirrel could smell or see caches). The order of the test trials, the side of the caching test cage, and the position of the laminate were counterbalanced across all squirrels according to the plan presented in Appendix B. During the habituation trials the observer had access to both olfactory and visual information of the location of nuts buried by the caching squirrel, that is to say the curtain was not used and all caches were present when the observer was given access to pilfer. During Test A the curtain was used to fully obstruct the view of the caching squirrel by the observer squirrel for the duration of the trial, but all caches were present when the observer was given access to pilfer. In Test B the curtain was not used so that the observer had full visual access to the cacher, but before the observer was given access to pilfer, all caches were removed and sawdust mixed between all cells in order to distribute remaining odour cues across all trays rather than where the caches were buried, and any soiled sawdust was removed. New unused sawdust was used at the start of each of the three experimental repetitions.

The caching squirrel's cage was set up according to the pre-determined schedule of Appendix B, with trays, laminate, nuts and curtain (if necessary) in position before allowing subjects into the test room. The observer squirrel was encouraged to enter the observing cage and rewarded with a single mealworm. Next the caching squirrel was allowed to enter the test cage containing the sawdust-filled trays to eat the hazelnuts without shells and cache the intact hazelnuts anywhere in the 16 uncovered cells. The duration of the caching trial was dependent upon how long it took the caching squirrel to eat and cache the nuts, up to a maximum of two hours; if the caching squirrel did not eat or cache within the first 15 minutes of entering the test cage it was planned that the trial would be suspended but at no time was this necessary. A time-constraint was set for each of the caching trials so that there would be a minimum delay for the observer squirrel to access the caches after witnessing them being buried. After each cache was made, if another was not made within the following 15 minutes the caching squirrel was immediately encouraged out of the testing arena and back to its home cage where it was always rewarded with a single mealworm. Within this time constraint the minimum number of caches made was one and the maximum was six. The experimenter then entered the caching cage, pulled down the curtain to obstruct the view of the observer (if it was not already drawn, as in Test A), removed the laminate from the covered cells, and removed any remaining un-consumed and un-cached nuts or empty shells. We then removed all cached items: during the two habituation-trials and during Test A new nuts were placed in the cells of the original caches (to enable the cacher to later recover their true caches, rather than replacements), and in Test A the curtain remained down; in Test B caches were removed and not replaced, the sawdust was re-distributed and finally the curtain was removed before the experimenter exited the test cage.

The observer squirrel was then allowed to enter the caching squirrel's cage via the small inter-connecting door, which was then shut, and the experimenter exited the test-room to resume remote monitoring. The observer remained in this cage until it had either found all of the caches (excluding Test B), searched all cells, or had been inactive for 15 minutes. The subject was then returned to its home cage.

Finally, we re-distributed the sawdust, removed soiled sawdust and replaced all of the original nuts in their cells to give the caching squirrel the opportunity to recover its own caches after the observer had exited the test room. The recovery trial ended after all caches were recovered or after 15 minutes of inactivity.

Behavioural measures

Behavioural data were collected for the duration of time that the observer had access to the caching cage. Owing to the nature of the video data it was not possible for the experimenter to remain blind to the condition or location of the caches during analysis.

The subject's accuracy of searching the testing arena was monitored as in Watanabe and Clayton (2007) as follows. In all trials one side of the total caching area was covered by transparent laminate so that the caching squirrels could only bury food in one side of the arena, either the front or rear cells.

According to Watanabe and Clayton the observers should preferentially search the correct side of the arena first if they remembered in which side of the arena the demonstrator had cached. Therefore we recorded whether the first search behaviour was on the correct side, i.e. the side that had not been covered by the laminate. We also recorded the proportion of time the observer spent engaged in search behaviour in the correct and incorrect sides of the testing arena in order to measure whether observers were exploring the cells equally or mainly searched the side that contained caches. Search behaviour was defined as sniffing the surface of the sawdust while stationary or while locomoting between cells, while not carrying a nut.

To determine the accuracy of pilferage, several additional measures were taken based upon pilferage efficiency and accuracy throughout the recovery trial (adapted from measures used by Watanabe & Clayton 2007). We defined an instance of pilferage (and pilferage attempt for Test B) as the subject having its head submerged in the sawdust substrate while engaging in digging behaviour. To assess *pilferage efficiency*, we recorded the following: the number of incorrect cells where attempted pilferage occurred before pilfering a correct cell that contained a cache (or attempting to pilfer from a correct cell in Test B); and the latency of pilfering a correct cell that contained a cache (or attempting to pilfer from a correct cell in Test B). To assess *pilferage accuracy* we recorded the following: whether the first pilferage attempt was in the correct location, a neighbouring location, the correct side only, or the incorrect location; and the distance of the first pilferage attempt to the nearest cache location (or cell that had previously contained a cache in Test B). Distance was measured to the nearest cm from where a nut had been cached in a cell to the location where the squirrel made its first pilferage attempt (where its head was submerged in the sawdust of a cell). We did not record all pilfer attempts, only the first, as during many trials the subject would employ a strategy of attempting to pilfer from every cell. According to Watanabe and Clayton the advantage of using measures based upon pilferage efficiency and accuracy, as opposed to the proportion of items recovered, is that we can compare the habituation trials and Test A with Test B when no food was present for the observer to recover.

Whether the observing squirrel had visual access to caches when they were being made was also monitored throughout the experiment via the remote viewing camera. Frequently the observer appeared to visually follow the behaviour of the caching squirrel, often frantically shadowing their movements from the adjacent cage. However, caches where the observer was facing away from the cacher while a nut was being buried are excluded from analyses for the conditions where visual access was available (a total of five caches were excluded from Test B; none needed excluding from the habituation trials). This has been done to reduce the possible effects of attentiveness on cache pilfering. In studies where the subject was not always observing caches various strategies have been employed, including directing the subjects attention to the position of the cache as it was being made by calling their name (Scheid & Bugnyar 2008; Scheid, Range & Bugynar 2007), or allowing caches to be observed only from restricted location to help to monitor which caches have been observed (Grodzinski, Watanabe & Clayton 2012).

Squirrels also made caches in non-tray locations during the study, and we could not prevent this. As these caches were clearly visible from the observing squirrel cage, we included these caches in the analysis (totalling two caches across all repetitions).

Analysis

This study used a one factor repeated measures design to examine the main effects of condition (olfactory cues and visual access, olfactory cues only, visual access only) upon each of the dependent measures. Data from habituation trial 1 was excluded from analysis as this served as a training period. Four subjects ($N = 4$) were tested in each of the three conditions: visual access and olfactory cues present, olfactory cues only, visual access only. Results from all three experimental repetitions are included in analysis.

GEEs were used for most of the analyses in this study for the reasons outlined in Chapter 2. All GEE analyses were carried out using a first-order autoregressive (AR(1)) working correlation matrix (for related measurements), and using pairwise comparison contrast tests with a Bonferroni adjustment for multiple comparisons. The best models are reported based on the Goodness of Fit statistic QIC and the corrected QICC model, with smaller values indicating a better fit.

Separate tests were conducted to assess the main effects of condition on each of the dependent measures. A GEE was carried using a binary regression with a logit link function for whether the first search attempt was made in the correct side of the arena. GEEs were carried out using a Tweedie regression (for a positively skewed distribution with scale and absolute zero values) with an identity link function for number of pilfering attempts, and distance of the first pilferage attempt to the nearest cache location. GEEs were carried out using an inverse Gaussian regression (for positively skewed data without absolute zero values**)** for latency to pilfer from the correct cell, and location of the first pilfer attempt (whether a correct cell, correct neighbouring cell, correct side of the arena, or incorrect side).

For analyses that did not accommodate a GEE model, separate repeated measures ANOVAs were used, namely the proportion of time the subject spent searching the front and rear of the testing arena. All reported data conform to assumptions of ANOVA (with equality of covariance matrices at a significance level above .001, and equality of error variances above .05, as defined by Pallant 2007).

Data were analysed using Microsoft Office Excel 2010 and SPSS 16.0 for Windows. Significant models are reported to a minimum of 5% alpha level.

Results

Search accuracy

There was a trend for subjects to search on the correct side of the arena (i.e., the one that had not been previously covered by laminate) more when they used olfactory cues only (M = .83, SD = .39, correct search attempts) compared to when they only had visual access alone (M = .33, SD = .49), or could use both types of information (M = .50, SD = .52), displayed in Figure 11. A GEE was carried out which showed QIC = 49.10, QICC = 48.73, reporting no significant effect of condition upon whether the first search attempt was made on the correct side of the arena (approached significance, *p* = .071).

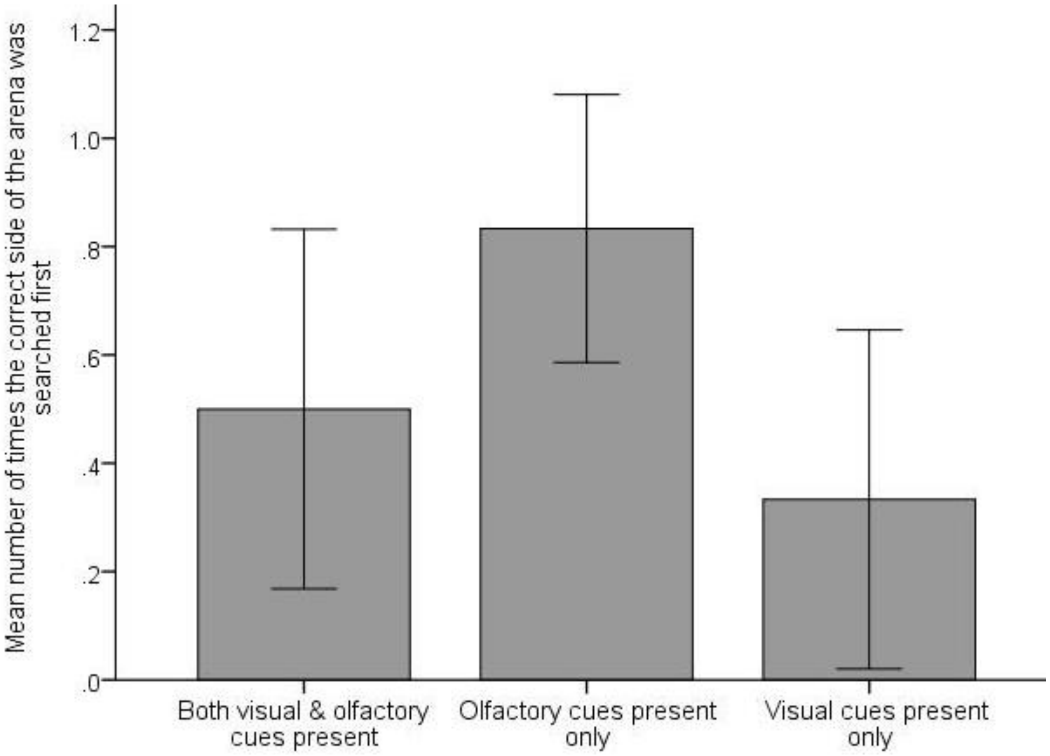


Figure 11. Number of times the first search attempt was made on the correct side of the testing arena, the side that contained (or previously contained, in Test B) caches, across conditions. Error bars represent 95% confidence intervals.

In terms of the amount of time the observer spent engaged in search behaviour in the front and rear of the testing arena, subjects spent on average 825 seconds searching the front section of the arena and 750 seconds searching the rear section of the arena, displayed in Figure 12. A repeated measures ANOVA was conducted which reported no effect of condition on the amount spent searching the front and rear of the testing arena (*p* = .313, observed power = .17).

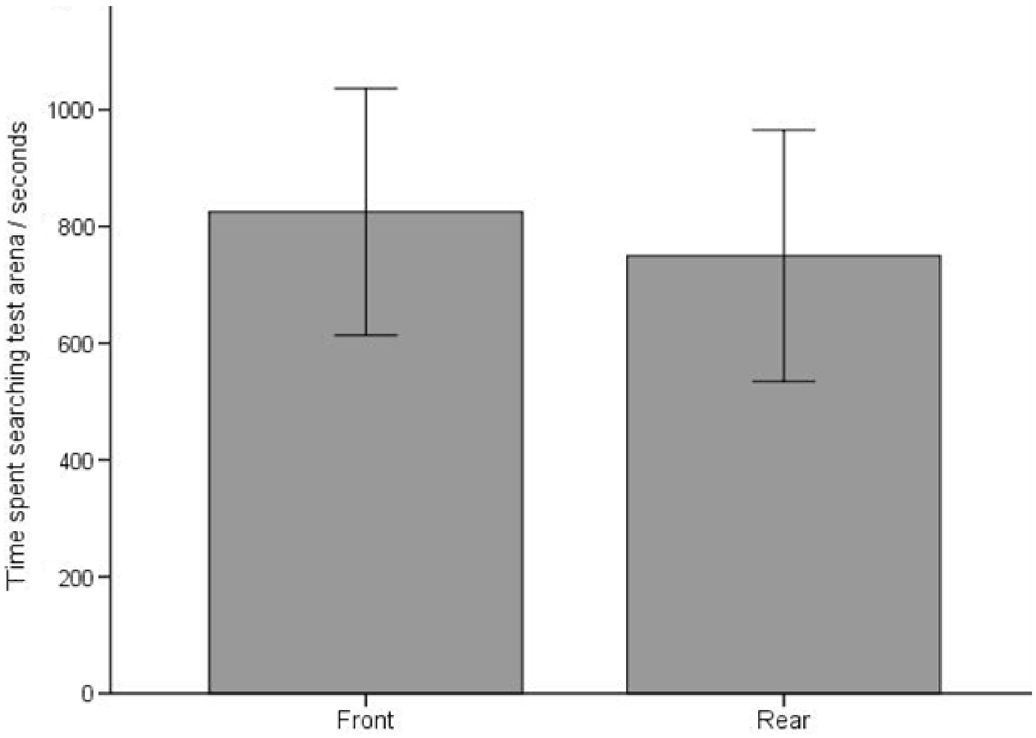


Figure 12. Time spent searching the front and rear cells of the testing arena, in seconds. Error bars represent 95% confidence intervals.

Pilferage efficiency

With visual access only squirrels attempted to pilfer from an incorrect cell an average of 4.60 (SD = 6.40) times before visiting a correct cell, compared to having olfactory cues only (M = .73, SD = .92), or a combination of both cues (M = .83, SD = 1.20), displayed in Figure 13. A GEE was carried out and showed QIC = 84.86, QICC = 87.01, reporting no significant effect of condition upon the number of pilferage attempts made (*p* = .112).

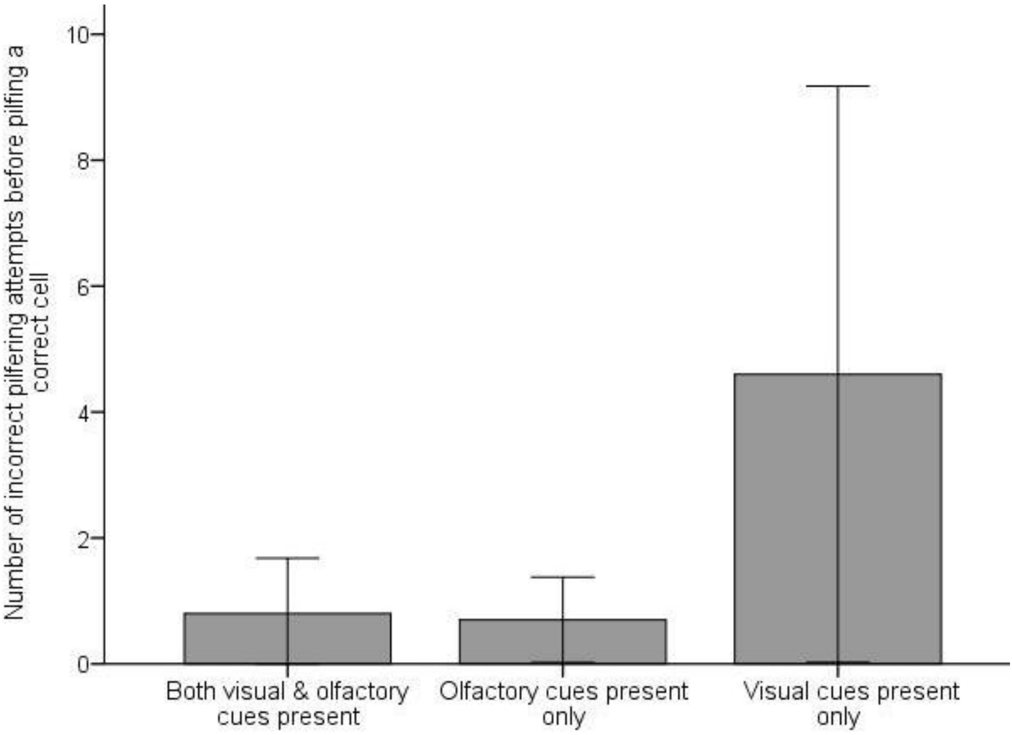


Figure 13. Number of incorrect pilfering attempts made before attempting to pilfer from a correct cell across conditions. Error bars represent 95% confidence intervals.

In terms of latency of making a pilferage attempt in a correct location, subjects were quicker to locate the correct cell when using both olfactory cues and also had visual access (M = 90, SD = 155 seconds) compared to when using olfactory cues alone (M = 219, SD = 382) or only had visual access (M = 196, SD = 202), displayed in Figure 14. A GEE was carried and showed QIC = 6.09, QICC = 6.87, reporting no significant effect of condition upon the time it took to locate a correct cell (p = .103).

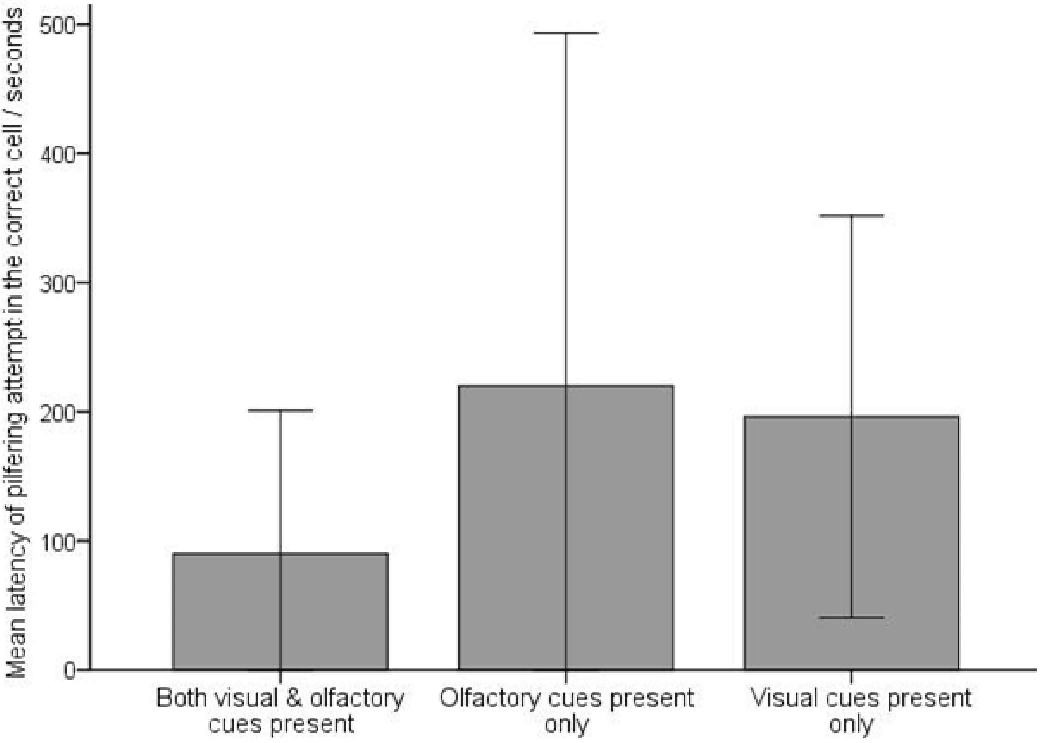


Figure 14. Latency, in seconds, to make a pilferage attempt from the correct cell, across conditions. Error bars represent 95% confidence intervals.

Pilferage accuracy

In terms of where the first pilferage attempt was most likely to occur, when using both cues combined 50% of attempts were made in the correct cell, and when using olfactory cues 50% of attempts were made in the correct cell. The remaining data for where the first pilfering attempt was made based on each location is displayed in Figure 15. A GEE was carried out which showed QIC = 9.92, QICC = 11.29, reporting that there was no effect of condition on where the first pilferage attempt was most likely to occur (*p* = .199).

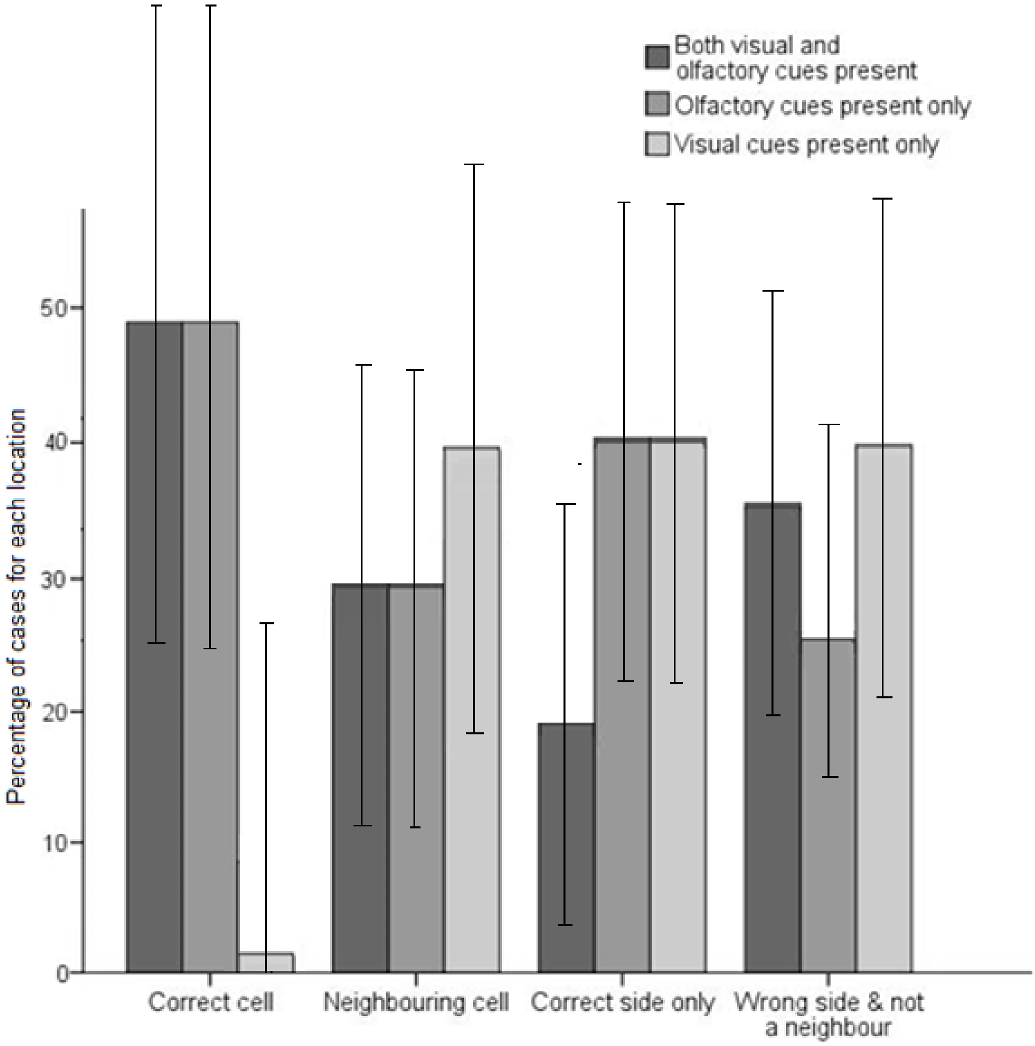


Figure 15. The percentages for the three conditions across each location where the first pilfering attempt was made. Error bars represent 95% confidence intervals.

When both visual access and olfactory cues were available the first pilfering attempt was made an average of 19cm (SD = 26) away from a correct cell; when olfactory cues only were available the distance to the correct cell was 16 (SD = 19), and when visual access was available M = 33cm (SD = 22), as displayed in Figure 16. A GEE was carried out which showed QIC = 297.82, QICC = 301.05, reporting that there was no effect of condition upon how far away the first pilferage attempt was made from a correct cell (approached significance *p* = .092). There was a trend for subjects to make their pilferage attempts closer to caches when using olfactory cues alone, in comparison to visual access only, or combined visual and olfactory information.

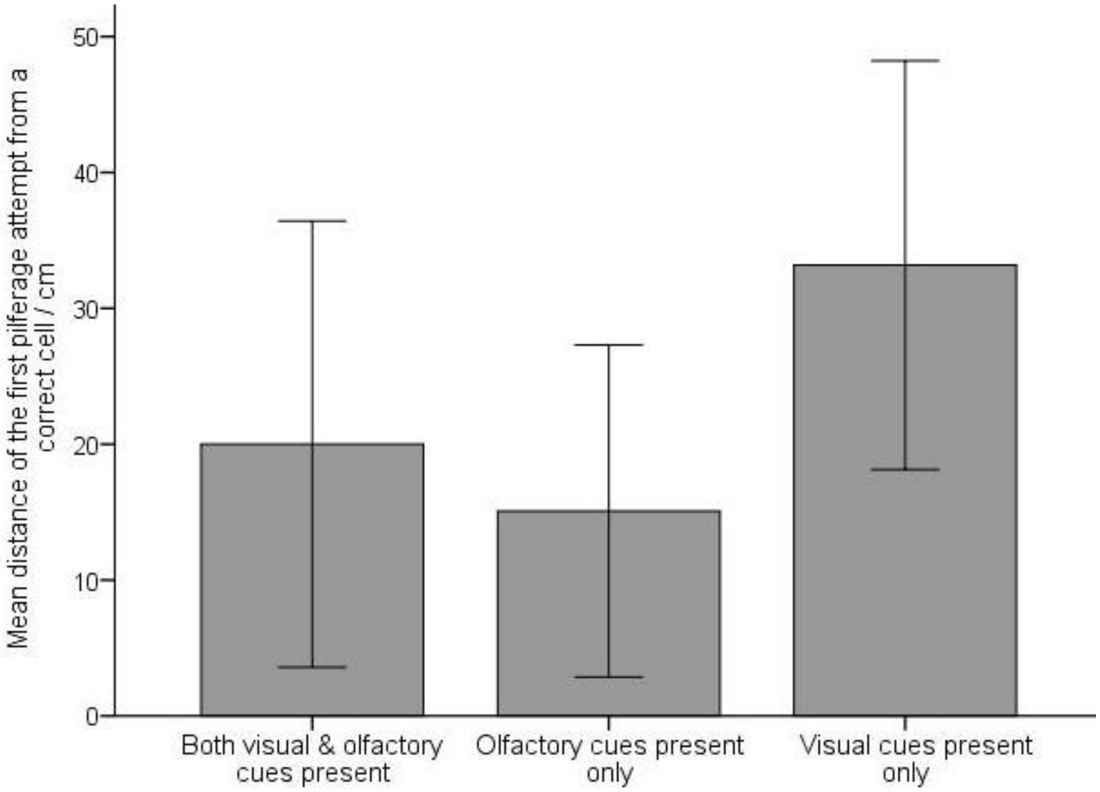


Figure 16. Distance of the first pilfering attempt from a correct cell, in cm. Error bars represent 95% confidence intervals.

Discussion

This was the first investigation of whether a rodent species uses OSM to aid cache pilferage. The results do not provide any evidence that squirrels use OSM to pilfer caches. In terms of search accuracy observers were more likely to search on the correct side of the caching arena when they were relying upon odour cues to locate caches than when relying on visual access or a combination of both types of information, however this this finding only approached significance. In terms of pilferage accuracy observers made their first pilferage attempt closer to the correct cell when relying upon odour cues alone as compared to using visual information or a combination of both cues, however this only approached significance. Although these differences between conditions were not significant, they were both in the opposite direction to those predicted by OSM; this makes it unlikely that the true population trend is in the direction of what would be predicted by OSM. The results suggest that OSM pays no part in grey squirrels' cache pilferage attempts, at least under the conditions of the present experiment.

Pilfering without OSM

Food storing rodents, parids and corvids have been shown to demonstrate pilferage reduction behaviour in the form of limiting visual information of the whereabouts of their cache sites. This suggests that onlookers pose a threat to cachers if they observe them storing food. Some species of corvid pose a threat to cachers because they can pilfer by OSM when they witness a cache. However, because pilferage behaviour has not been investigated in many other non-corvid species it was unclear whether onlookers of other caching species may pose the same risks to caches by pilfering using OSM. Grey squirrels were not found to pilfer caches using OSM in our current study, but showed some preference for using olfactory cues.

Among the species that have been experimentally investigated in OSM studies, jackdaws, grey jays and black-capped chickadees have been reported to fail in OSM tasks. Jackdaws are not specialised cachers and they do not depend upon hoards for their long-term survival, and thus engaging in cache protection behaviour would be more costly than the benefits gained from caching. However, grey jays and black-capped chickadees are specialised cachers, dependent upon their stores, and they live in social groups during the caching season so there is a high opportunity for witnessing conspecifics making caches. Hitchcock and Sherry (1995) report that in captive studies of black capped-chickadees pilferage is not that common, and they suggest that cache theft by conspecifics might be a rare occurrence in wild chickadees, thus these birds are unlikely to possess OSM. Nevertheless black capped chickadees have been reported to limit their caching in the presence of conspecifics; Stone and Baker (1989) suggest this helps them to limit opportunistic pilferage, as opposed to pilferage by observation, because there are fewer other foragers in the vicinity. Similarly, grey jays have been reported to demonstrate evasive behaviour and limit or cease their caching when in the presence of heterospecific pilferers but not conspecific pilferers (Burnell & Tomback 1985). Burnell and Tomback suggest that grey jays have evolved this strategy in response to Steller’s jays because this species are thought to frequently pilfer from grey jays, while other grey jays do not frequently steal caches from one another. Because cache pilferage is not a problem within each of these species, they are unlikely to possess OSM.

On the other hand, captive studies of grey squirrels report that they recover caches that they have not made themselves (e.g., McQuade et al. 1986; Macdonald 1997; the current data), so it appears that pilferage is much more frequent in this species and may be a problem to cachers. Given that they do not appear to use OSM to steal caches they have witnessed being made, future studies should explore by what other means grey squirrels, and indeed other cache pilfering species, engage in cache pilferage.

Given that grey squirrels change their behaviour in response to a conspecific audience it is highly likely that conspecifics do pose a threat to caching squirrels. However, the risk of being observed by a conspecific while caching might be different for squirrels as it is in those species that possess OSM. Hopewell, Leaver and Lea (2008) present data that suggests squirrels might primarily respond to conspecifics as competitors for resources rather than as pilferers of their caches. Thus, orienting oneself away from an onlooker while burying food might help to reduce the risk associated with competition, such as having food stolen while caching by a more dominant individual. Bugynar and Kotrschal (2002) suggest that raiding of food caches in species that do not use OSM is achieved when the cacher is still present and when the pilferer is the more dominant individual. Thus immediate pilferage can be achieved by a more dominant individual using local enhancement cues (Gibb 1960). In species that use OSM on the other hand, the observer can delay raiding until the cacher has left the area, which then allows subordinates a means to compete indirectly for food without physically displacing dominant individuals (Armstrong et al. 2012; Dally et al. 2005a). The role of competition in caching behaviour is discussed further in Chapter 4.

Comparing squirrels with corvids

Of the studies of various corvid species, the majority conclude that they possess some degree of OSM. Given that onlookers can return to pilfer caches after a delay simply by observation, this helps to explain why corvids engage in pilferage reduction behaviour that seeks to minimise the opportunity for onlookers to witness caches being made (for the most recent review see Grodzinski & Clayton 2010). This illustrates Bugnyar & Kotrschal's (2002) argument that within species cachers and pilferers evolve different strategies to compete with one another according to the selection pressure; caching individuals evolve behaviour to minimise the risk of cache pilferage, which has selected for pilferers to evolve strategies that allow them to pilfer more easily. In corvids, this has selected for OSM. On the other hand, in grey squirrels the adaptive pressures might have resulted in the selection of different pilferage strategies, such as pilfering immediately after observing a cache (witnessed in grey squirrels by Steele et al. 2014); such a strategy could be aided by being a more dominant individual, which we know squirrels use to access food resources (reviewed in Chapter 4). This requires further investigation to fully understand the specific risks that conspecifics pose to grey squirrels, a question that is addressed more fully in Chapters 4 and 6.

An important point to consider is that the study design is likely to have contributed to the outcome of the study. We used methodology adapted from the corvid literature. However the actual food storing behaviour of corvids is very different from that of squirrels. For instance, corvids do not have the same sensitive sense of smell as rodents, with smaller olfactory bulbs, and thus olfaction is used less in cache retrieval and pilfering than in rodents (Vander Wall 1988). Magpies (Buitron & Nuechterlein 1985) and ravens (Harriman & Berger 1986) can use olfaction to detect caches but odour cues tend not to be used to enable cache recovery (discussed in Male & Smulders 2007a). Although previous research has shown that grey squirrels have a preference for recovering their own caches using visual cues over olfactory cues (McQuade et al. 1986), in the current study because using visual information was not always reliable (i.e., on trials where the nut was removed), the observer might have favoured using odour cues as opposed to using OSM; indeed there was a trend for this in the data, but we cannot conclude that this is the case with such a small sample size and non-significant effects. Designing an experiment without odour cues might provide a more ecologically relevant situation in which rodents might make use of OSM, rather than adapting a study that is more suited to avian cachers.

The problems with laboratory caching studies

The largest drawback of this study (and those presented in Table 6) has already been outlined in Chapter 2, namely that captive testing arenas cannot represent natural caching behaviour in an ecologically realistic way. Natural caches made in the wild are spaced at much greater distances, and onlookers are often much farther away compared to in a laboratory testing arena. In addition, the costs and benefits of caching for captive animals are not the same as for their wild counterparts. If caches are not made the captive individual still has a reliable supply of food; if caches are lost, more cacheable items will be presented; and if an observer does not steal a cache it will not go hungry. As well as reducing motivation to cache, recover and pilfer, conditions of captivity could also reduce the motivation (or indeed ability for those housed alone) to engage in pilferage avoidance behaviour. Therefore we might not be seeing an accurate representation of the caching and pilfering behaviour that would be expected in wild populations. Future research should aim to investigate caching decisions in wild animals; though observing natural caching behaviour can be more time-consuming, and restricted to peak caching seasons (at least in seasonal cachers like grey squirrels), it would provide much more ecologically relevant data to study squirrels in the future as well as corvids.

Using laboratory housed grey squirrels, in particular, is also problematic for several reasons. Being a non-domesticated species they require considerable effort and hand-rearing from a very young age to habituate to captivity. They have substantial housing requirements to maintain their natural behaviour and prevent escapees, for the most part being housed singly, and even with all this they do not always thrive. For these reasons it is difficult to achieve large enough sample sizes for experimental studies, meaning that studies are often repeated measures with observers and pilferers partaking in both roles in the same experiment; moreover, individuals tend to be re-tested between studies that investigate similar behaviour which could affect the internal validity of the research. This again, is a common feature of many laboratory studies that investigate food hoarding behaviour.

It is essential that future research is carried out on the pilferage behaviour of caching species, particularly with other taxa that demonstrate pilferage avoidance behaviour, in order to understand whether similar adaptive pressures have led similar caching and pilferage strategies among different species. This study is valuable in that it is the first to experimentally investigate the use of OSM by grey squirrels, and as such it is the first to explore the use of OSM by a mammalian caching species. Unfortunately there were several drawbacks that prevented strong conclusions being drawn, the most notable of these being sample size. Nevertheless, previous studies that have reported OSM have been subject to the same experimental difficulties; Watanabe and Clayton's (2007) study used an sample size of seven observers and still reported evidence of OSM. This suggests that studying more laboratory squirrels would simply allow us to conclude with more certainty that grey squirrels do not possess OSM.

Conclusion

In conclusion, though OSM has long been acknowledged as a possibility by those interested in food hoarding species, the behaviour of pilferers has not received nearly as much interest as the behaviour of cachers. The evolutionary pressures of food storing cannot be fully understood without understanding cache loss, and how this is prevented and achieved within species. In the current study we have shown that grey squirrels do not use OSM to pilfer caches in a laboratory setting. Given that previous studies have shown that they adjust their behaviour in ways to minimise cache theft in the presence of observers, it is more likely that they do this to prevent immediate pilferage by conspecifics but field studies would help to clarify this. The current study provides a basis for exploring different strategies used by grey squirrels and other species that engage in cache pilferage.

Chapter 4: Dominance effects on caching in wild Eastern grey squirrels.

Introduction

Foraging squirrels face a trade-off between resource competition, pilferage risk and predation risk: an individual squirrel must respond flexibly to competitors at a food patch (Hopewell et al. 2008), so that aggressive encounters with conspecifics are avoided, and food acquisition is maximised; they should cache as much food as possible whilst ensuring that caches are at lowest risk of theft by conspecifics (Macdonald 1996); and must also minimise the potential for predation by heterospecifics (Lima et al. 1985). Grey squirrels have been shown to adjust their foraging and caching behaviour in response to social and predatory risks (reviewed in Chapters 2 and 6 respectively) in a similar way to some food caching birds. Among food hoarding birds social dominance has also been found to have a large influence upon individual caching strategies; those differing in social rank adopt different methods of sequestering, storing and recovering food in response to pilferage and predation risks. There is some evidence to suggest that grey squirrels have a clear dominance structure, however, it is not known whether they also employ different foraging and hoarding strategies based upon social rank in the same way as caching birds. The current study has addressed how dominance influences foraging strategies among different ranking grey squirrels and whether there are individual differences in their food hoarding and cache protection behaviour in relation to social and predatory risks.

Social dominance in food storing birds

Many scatter hoarding birds tend to live in small groups structured by rank, where there are a lot of opportunities for witnessing conspecifics storing food, as well as a high risk of losing stored food to competitors. Chapters 2 and 3 discuss some of the ways individuals can reduce costs associated with social foraging and cache loss. For species that forage in dominance structured groups, relative social rank can influence individual hoarding strategies. Within the Paridae and Corvidae social dominance has been suggested to affect food hoarding behaviour in two ways: scatter hoarders compete for access for food to store when they are foraging, and also when they are recovering caches of their own or conspecifics (Clayton et al. 2007). Brodin et al. (2001) suggest that individuals of differing social rank behave differently in the way that they forage, cache and retrieve food. More dominant individuals use their status to monopolise food supplies at the source as well as recovering their own and subordinates’ caches, while lower ranking individuals cannot pilfer the food hoards of those more dominant and so need to invest more energy in hiding caches which they cannot defend from dominant thieves. A variety of studies have shown how different caching strategies are found between dominant and subordinate birds in order to achieve optimal energy gain from hoarding. For instance, compared to subordinates, dominant birds use aggression to protect their caches (pinyon jay: Bednekoff & Balda 1996a; raven: Bugnyar & Heinrich 2005; Bugnyar & Kotrschal 2002; Eurasian jay: Goodwin 1956; Dally 2004; Western scrub-jay: Dally et al. 2005a), forage in more preferred locations (willow tit: Hogstad 1988), and supplant others while they are burying food (Eurasian jay: Shaw & Clayton 2012a). Subordinates on the other hand, supress caching in the presence of other birds (New Zealand Robin: Burns & Steer 2006), opting to cache where there are fewer conspecifics (Eurasian jay: Shaw & Clayton 2012a).

Social dominance in food storing rodents

Despite not having a similar group living structure as some caching corvids and parids, there is evidence that social dominance may affect hoarding behaviour in food storing mammals that forage at the same patch. Some between species comparisons show that more dominant individuals prefer to larder hoard because they can use aggression to defend their stores (chisel-toothed kangaroo rats and Merriam's kangaroo rats were dominant over dark kangaroo mice and long-tailed and little pocket mice: Jenkins & Breck 1998). Similar strategies have been found within species with dominants more likely to larder hoard and pilfer the stores of others (Eastern chipmunk: Clarke & Kramer 1994; red squirrel, *Tamiasciurus hudsonicus*: Gerhardt 2005). There has been very little study of how dominance relationships affect food hoarding and cache protection behaviour among grey squirrels. There is evidence that they engage in similar cache protection behaviour to birds and that conspecific presence signals pilferage risk (reviewed and experimentally tested in Chapter 2). However, since they do not seem to use OSM to pilfer caches like corvids (reviewed and experimentally tested in Chapter 3), it is unclear what pilferage strategy would warrant behaviour that serves to reduce pilferage by observation. It has been reported that squirrels can immediately pilfer after witnessing a cache being made (Steele et al. 2014), something which being a more dominant individual could benefit because there would be less risk involved. Accordingly this would also support the view that some cachers would need to engage in strategies that minimise the possibility of this occurring, namely subordinates.

Grey squirrels are mostly asocial (Koprowski 1996), they do not share their food hoards with kin (Spritzer & Brazeau 2003), and they actively engage in behaviours to minimise the loss of their caches to pilferers (reviewed in Chapter 2), suggesting they do not willingly share their food hoards (Leaver et al. 2007). However, they are non-territorial with overlapping home-ranges and so come into frequent contact with other squirrels while foraging at the same food patch (Lewis 1980; Vander Wall & Jenkins, 2003). Therefore, despite being asocial, hierarchies appear to exist among individuals that frequent the same foraging patch. A number of studies have reported that grey squirrels demonstrate a stable linear dominance hierarchy, and use their physical attributes to monopolise food patches, with larger mature males relying on aggression to dominate females and younger subordinate males (Allen & Aspey 1986; Flyger 1955; 1960; Horwich 1972; Koprowski 1996; Pack et al. 1967; Taylor 1966; Thompson 1978). What is less clear from this research is whether lower ranking squirrels employ strategies to offset the increased competition they face. Some research shows that grey squirrels might act in ways to compensate the additional competition for resources when foraging in the presence of conspecifics; grey squirrels have been found to increase their foraging time when conspecifics are present compared to when they are absent (Hopewell et al. 2008). Other research shows that some grey squirrels act in ways that might serve to limit antagonistic interaction with foraging conspecifics, such as transporting food away from a food patch (Spritzer & Brazeau 2003), increasing vigilance levels to identify potential competitors (Tarigan 1994), and monitoring the auditory presence of conspecifics (Partan et al. 2010; Partan et al. 2009).

In a similar vein to what has been reported in birds, grey squirrels might also be sensitive to dominance networks while they are storing food. Spritzer (1999) reports anecdotal observations of squirrels aggressively defending their caches. Currently, however, there is only one observational study that suggests there might be a link between social rank and caching behaviour of the grey squirrel: Leaver et al. (unpublished data) noted that dominant individuals appear to cache differently to subordinates, with more dominant grey squirrels clumping their caches while subordinate individuals distribute their caches more widely. From this study, it seems that the higher ranking individuals may be more able to aggressively defend their caches, whereas subordinates may need to rely on other pilferage avoidance mechanisms such as those based upon social information at the time of caching. For example, squirrels that change their food hoarding when conspecifics are present could be doing so to minimise competitive interactions (e.g.: caching less: Leaver et al. 2007; eating more: Steele et al. 2008; storing food in out of sight locations: Leaver et al. 2007; Steele et al. 2008) and to protect their caches from pilfering dominant squirrels (making more interruptions to caching: Hopewell & Leaver 2008; Steele et al. 2008; spending more time disguising caches: Hopewell & Leaver 2008; and spacing caches father apart from one another: Leaver et al. 2007). Accordingly, the first research question of the current study was whether there were individual differences in the foraging and hoarding behaviour of the grey squirrel and whether this is related to their dominance structure. More specifically, we investigated whether subordinate individuals engaged in more cache protection behaviour than dominants, including making more curtailed digs, facing away from conspecifics or behind visual barriers when caching, and caching where there was fewer conspecifics.

Effects of dominance upon decisions about pilferage risk and predation risk

It is clear that the social environment presents several problems to food storing species: competing for resources with conspecifics, avoiding aggressive encounters, and minimising pilferage risk, all of which should cause them to be wary of foraging at patches where there is a higher density of competitors, particularly for a less social species like the grey squirrel. However, at the same time, individuals must minimise their risk of being predated, the optimal conditions for which frequently conflict with securing food resources; for instance, studies of the dilution effect frequently show that predation risk can be reduced when foraging among many individuals (Bednekoff & Lima 1998; Elgar 1989; Galef & Giraldeau 2001; Rausch, Siu, Stevenson, Sydnor 2012). Since areas of vegetation will attract competitors because they provide both a source of food and a means of cover and escape from predators, therefore squirrels could benefit from the presence of other foragers in terms of predation risk.

Though a number of studies have investigated how predation risk affects general foraging or hoarding efficiency (e.g. Daly, Wilson, Behrends & Jacobs 1990; Leaver 2004; Steele et al. 2014; Valone & Lima 1987), fewer have incorporated the role of dominance structure in response to predation risk. There is some evidence to suggest that in dominance-structured groups of birds the risk of predation affects dominants and subordinates differently. Subordinate flocking willow tits have been found to forage in riskier places (Ekman 1987; Koivula et al., 1994), and transport food farther from the source and cache in more exposed locations than dominants (Lahti et al. 1998). Such behaviour reduces foraging competition with dominants and the risk of cache loss but increases the risk of predation. It seems that because subordinates are restricted by dominants in where and when they can forage and cache, they must take higher risks, while dominants can monopolise patches of lower predation risk (Lange & Leimar 2001). There is also some research to show that dominant food storing birds carry less fat reserves than subordinates, which makes them less of a target to predators (Lundborg & Brodin 2003). Birds with greater fat stores are at a higher risk of being killed by a predator because of reduced in-flight manoeuvrability (Witter & Cuthill 1993), and an increase in fat requires more foraging, which is performed at a cost in time spent being vigilant (Lima & Dill 1990). On the other hand, dominant individuals can invest more into their external energy stores (Lucas et al. 2001) such as by caching more and protecting their hoards.

Scatter hoarding rodents are known to transport food to locations where the probability of pilferage is reduced (Muñoz & Bonal 2011; Stapanian & Smith 1986; Steele et al. 2014). Several studies report that grey squirrels adjust their foraging behaviour in response to predation risk, for example, by reducing their foraging time in more exposed locations compared to areas of cover (Brown et al. 1992; Booth, et al. 2012; Bowers et al. 1993; Newman et al. 1988) or transporting food to cover to eat and cache (Lima & Valone 1986; Lima et al. 1985). However both of these types of study typically only consider the trade-offs between the benefits of limiting pilferage or predation separately against the energetic costs of where to place caches. In reality, for wild-living individuals these two trade-offs are likely to be highly connected. To date, only one study has reported that there might be a trade-off between minimising the risks of predation and reducing the risks that competitors pose. In the first part of their study Steele et al. (2014) found that artificial caches buried close to trees were at higher risk of cache theft compared to those buried in the open. This suggests that, in terms of cache longevity, it is profitable to store food in areas of higher predation risk. In the second part of their study they found that when storing a profitable food item grey squirrels would preferentially cache in open areas that were higher in predation risk, compared with when they were storing non-profitable items. This study demonstrates how decisions about predation risks can be closely connected to the pilferage risks posed by competing conspecifics.

Furthermore, because research indicates that squirrel hoarding behaviour is influenced by social dominance, then it is likely that this pilferage-predation risk trade-off will also be influenced by social dominance. When making cache-placement decisions dominants and subordinates are likely to trade-off these risks differently, with subordinates exposing themselves to increased predation risks by placing their caches in more exposed locations to protect them from pilferage, compared to higher ranking individuals who can use aggression to increase their access to food. While there is evidence to suggest that food storing birds might be behaving this way, this has not been studied in grey squirrels. In comparison to some of the caching birds studied, grey squirrels are obligate long-term scatter hoarders and are highly dependent on the long-term survival of their stores; they are therefore likely to be under strong selection pressure to make optimal adjustments to their caching behaviour in response to social dominance and predation risk.

Grey squirrels: social dominance, pilferage risk and predation risk

From the literature reviewed here it is apparent that grey squirrel food hoarding behaviour is similar to that of some avian cachers in a number of ways: they demonstrate social hierarchies that influence their foraging access; they adjust their behaviour to conspecific audiences in ways that might help to reduce pilfering of their caches; and they incorporate predation risk into decisions about cache placement. The current study addresses whether social hierarchies play a role in the caching behaviour of grey squirrels and whether dominants and subordinates behave differently in response to competition, pilferage risk and predation risk; with subordinates more likely to act in ways to reduce pilferage but in doing so increasing their exposure to predators. Understanding whether those differing in social rank behave differently while caching, might also help to reveal more about the pilferage behaviour of grey squirrels. We know that food storing birds use a variety of strategies to pilfer, such as exerting social dominance to displace cachers, and sometimes they use OSM, but little is known about pilferage in grey squirrels. Since squirrels demonstrate social hierarchies, it is possible that they are engaging in similar dominance-based pilferage strategies to some species of flocking birds. This would help to clarify why they engage in pilferage avoidance behaviour, though do not appear to use OSM.

In the current study, dominance interactions were measured in wild squirrels at a provisioned food source in order to confirm that the study population was composed of a linear hierarchical structure as previously found for grey squirrels. Using aggression, chases and displacement behaviours as measures of dominance, it was predicted that higher ranking individuals would sequester more food while subordinate individuals would cache more food.

Cache placement was monitored in order to determine where squirrels preferred to cache as a function of three different risk factors:

(1) *caching distance from a provisioned food source* provided a measure of competition avoidance since at the source there was a high density of conspecifics;

(2) *caching distance from conspecifics* when the conspecifics were oriented toward the cacher provided a measure of effort to avoid pilferage risk;

(3) *caching distance from refuge* was measured as an assay of a squirrel's willingness to expose itself to predation risk.

It was predicted that compared to dominants, subordinates would cache farther from the food source to avoid competition, farther from on-looking neighbours in an effort to reduce pilferage risk, and farther from cover as they would be less risk-averse than dominant individuals.

Given that there is a trade-off of where caches are placed in relation to risks of pilferage, competition and predation, we investigated whether squirrels modified their use of pilferage reduction behaviour in relation to where caches were placed and in relation to their social ranking. Pilferage reduction behaviour included behaviour previously been reported to be used by caching grey squirrels (reviewed in Chapter 2), including how many curtailed digs were performed when caching, whether the cacher faced toward or away from conspecifics while caching, and whether they cached behind a visual barrier or not. In relation to where caches were placed, the individual predictions for each pilferage reduction strategy is presented in Table 7; while in relation to squirrel identity we predicted that overall lower ranking individuals would make more use of pilferage reduction strategies while caching in comparison to those that were higher ranking.

Table 7. *Predictions of which pilferage reduction strategy would be used by cachers depending upon if they act primarily in ways to limit pilferage risk, competition, or predation risk.*

Hypothesis based upon distance to risk of…	**Whether pilferage reduction strategy is used while caching:**		
	Curtailed digs	**Caching orientation**	**Use of visual barrier**
Cache pilferage	More curtailed digging minimises the possibility for pilferage.	Facing away from conspecifics minimises the possibility for pilferage.	Using a visual barrier minimises the possibility for pilferage.
Competitive interaction	Fewer curtailed digs means caches can be made more quickly, so minimising exposure time to a competitor.	Facing onlookers allows the cacher to monitor their positions.	Avoiding using a visual barrier allows the cacher to monitor the positions of competitors.
Predation	Fewer curtailed digs means caches can be made more quickly, thus minimising exposure time to predators.	Facing towards onlookers helps to monitor the vigilance of onlookers to potential predator cues.	Avoiding using a barrier allows the cacher to monitor the vigilance of onlookers to potential predator cues.

Method

Ethics and licensing

Trapping was carried out in accordance with the ‘Association of Animal Behaviour Guidelines for the Use of Animals in Research’, the University of Exeter Psychology Ethics Committee, and under a Natural England permit to live trap and release.

Trapping of subjects

Trapping and observations were carried out during the peak food hoarding season from September through December 2011 at Streatham Campus, University of Exeter, Devon, UK. An area of campus was chosen (latitude N50:44:03, longitude W3:32:13) that was approximately 60 x 25 metres and predominantly consisted of evergreen and deciduous nut-bearing trees and rhododendron bushes with a clearing in the centre where squirrels tended to forage and cache. Ten traps (Tomahawk Live Trap, Wisconsin, U.S.A., model #202) were spaced in sheltered areas around this site, baited with peanut butter and checked at 1-2 hour intervals. When a squirrel was trapped, it was weighed (juveniles < 405g, adults > 535g, as per Heller 1978), sexed, PIT tagged, and its fur was marked in a distinctive pattern (e.g., back spot, side crosses) with black hair dye, before being released at the same location in which it had been trapped. A total of 17 squirrels were marked but not all were subsequently observed engaging in competitive or caching behaviour. Accordingly, 9 were included in the competition data and 11 were included in the in the caching data of this study.

Design and procedure

At the start of each observation session 100 hazelnuts in shells were placed on a tree stump (approx. diameter 1m) in the centre of the observation site. A video camera was positioned 3m east of the tree stump facing the provisioned food and an observer sat 20-25m north of the tree stump. Observations were conducted from approximately 09:30 and/or 14:00, and each session continued until all of the hazelnuts were gone (M = 1h 14m, SD = 29m) or for a maximum of two hours. Approximately 40 hours of data were collected in 36 observation sessions over 26 non-consecutive days.

Dominance interactions

During observations and from the videos that were collected, data were obtained relating to dominance interactions between squirrels at the site of the provisioned food (the tree stump). Records were made each time a chase occurred between two squirrels in the observation area, or an attempted displacement was made at the provisioned food. The identity of both the chaser/displacer and the squirrel that was being chased/displaced was recorded, and also whether the chase/displacement was successful, i.e., whether the chasing/displacing squirrel successfully prevented the other squirrel from accessing the provisioned food during that specific interaction. If the chase/displacement was not successful the chaser would be considered to have lost the interaction. The criteria we used to define interactions are provided in Table 8.

Table 8. *Criteria for dominance. Each time a squirrel attempted to gain access to food in the presence of another squirrel, this was recorded as one behavioural event, with one winning squirrel (dominant) that gained or maintained access to the food and one losing squirrel (subordinate) that did not have access or lost access to the provisioned food source, or made an unsuccessful displacement attempt (adapted from Allen & Aspey 1986 and Thompson 1978). Only chases/displacements that occurred at the provisioned food source were included in analysis, so that we could exclude behaviour that was potentially unrelated to dominance. At no point was there more than one squirrel at the food source without an antagonistic interaction occurring.*

Dominance interaction	**Dominant**	**Subordinate**
Two squirrels approach the provisioned food source; Squirrel A waits for Squirrel B to take a nut first.	B	A
Squirrel A is at the provisioned food source and Squirrel B approaches. Squirrel A leaves the food source in response to the approach or presence of Squirrel B, or Squirrel A is chased away by Squirrel B. Such behaviour has been operationally defined as a displacement according to Hopewell et al. (2008) “where one squirrel moves out of the nut patch when approached by another” (p. 1145).	B	A
Squirrel A approaches the food source where Squirrel B is already located. Squirrel B prevents Squirrel A from accessing the food either by: B chasing A away from the provisioned food; or, B performs vigilant behaviour directed at A in the form of raised fur and tail, often accompanied by vocalisations, and Squirrel A retreats from the food source.	B	A
If the previous scenario is displayed but the receiver Squirrel A does not retreat from the food source as a direct result of the presence of Squirrel B, then Squirrel B is said to have lost the interaction encounter.	A	B

Caching data

Collecting data on cache placement allowed us to see how this varied in response to pilferage risk, competition risk and predation risk. Caches were operationally defined according to a description adapted from Steele et al. (2008), Laidler (1980) and Macdonald (1995) which is presented in Table 5, Chapter 2.

During observations, the observer recorded data onto a check sheet which consisted of a scale map of the observation site, illustrating the positions of trees and shrubbery (Figure 17). This enabled the following records to be made each time a cache was made by a marked or unmarked squirrel: the time the cache was made; the identity of the caching squirrel (marking, age, sex); the location of each cache, including distance from the provisioned food (as an assay of competition risk), distance from nearest facing neighbour (as an assay of pilferage risk), and distance from nearest escape tree (as an assay of predation risk); whether the cached nut was a provisioned hazelnut or not; the orientation of the squirrel while caching (cardinal direction and relative to other squirrels: facing toward or away from their nearest neighbour as defined in Leaver et al. 2007); the presence of other squirrels at the observation site at the time the cache was made, including the number, location, orientation and identity; whether there was a visual barrier (e.g., a shrub) between the caching squirrel and their nearest neighbour at the time of the cache; and finally, the number of curtailed digs made prior to caching, including total number made prior to each cache.

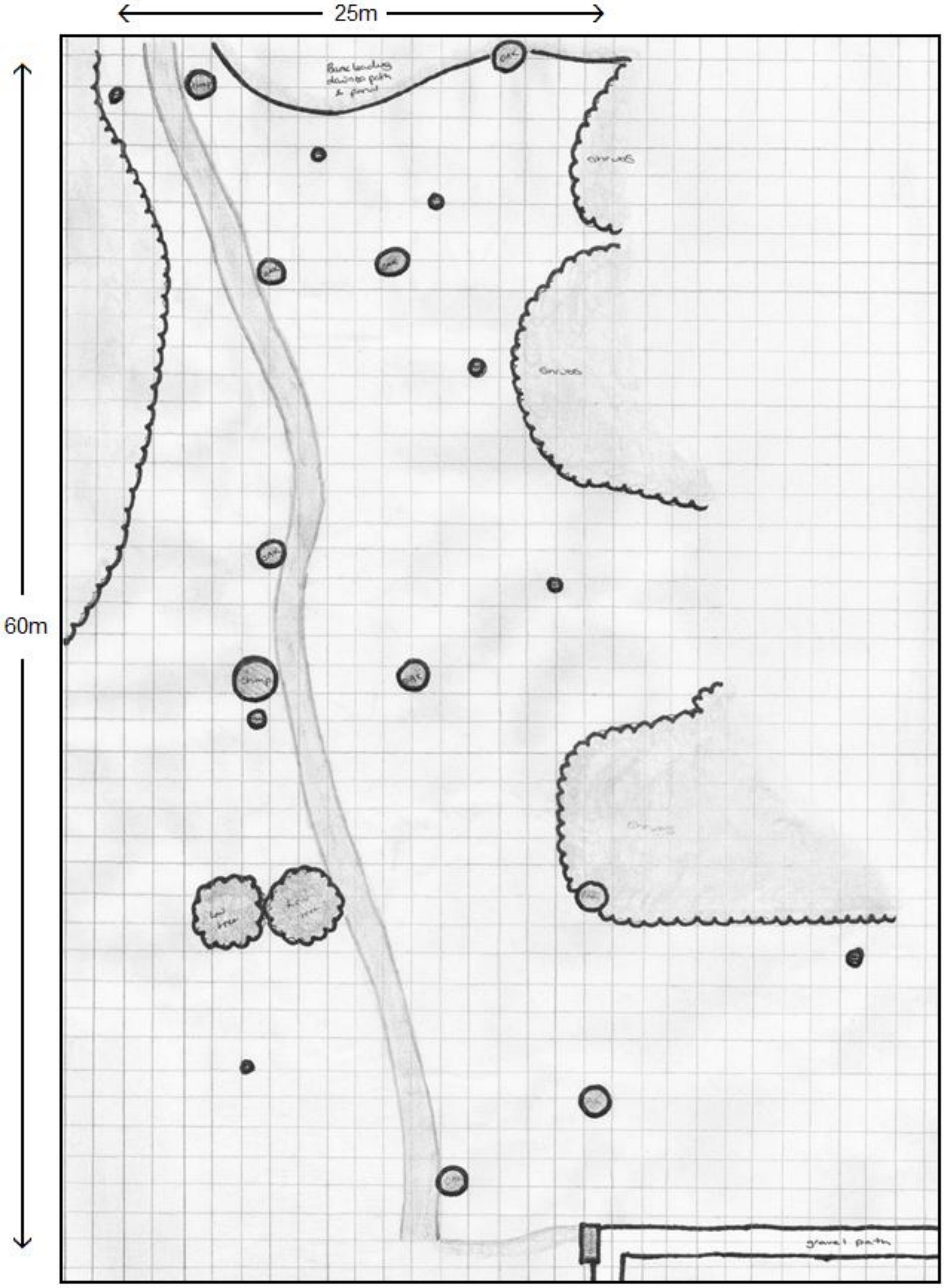


Figure 17. Map of observation site. Also used as an observation check sheet to record the location of each cache and other information at the time of the cache. Each square represents approximately 1.5m^2.

Statistics

The dominance interactions allowed us to generate a social network of who consistently supplanted whom at the provisioned food. These data were analysed using UCINET version 6 (Analytic Technologies, Kentucky, USA) and also using the methods reported in Lehner (1998) for analysing linearity (p. 332-335). Cache placement distances to the food source, neighbouring squirrels, and refuge analysed for differences based upon dominance rank. Statistical tests reported from these data have been calculated predominantly using non-parametric methods (a Kruskall-Wallis analysis) due to a substantial skew in the data.

We used SPSS Version 16.0 to carry out statistical analysis for the data on cache placement. All of our measures were checked for outliers, skew and normality; where violations were apparent and transformations unsuccessful (Kolmogorov-Smirnov $p < .01$, advised in Pallent 2007), we carried out a Generalized Linear Model (GZLM). We applied a backward elimination process resulting in a minimum adequate model with the lowest Akaike's Information Criterion (AIC) for assessing model fit; selecting the model that was most efficient at explaining the variance in the data. Based upon our hypotheses we were interested in three types of pilferage reduction behaviour: the number of curtailed digs made prior to caching, whether a visual barrier was between the cacher and their nearest neighbour, and the facing orientation of the caching squirrel from their nearest neighbour. We investigated whether these pilferage reduction behaviours were displayed depending upon cache placement. Three GZLM's were carried out which included the following measures of cache placement as predictors of pilferage reduction behaviour in each model: caching distance in metres to cover (exposure to predation risk), caching distance in metres to food source (risk of competition), and caching distance in metres to nearest neighbour that was orientated toward the caching event (effort to avoid pilferage risk). Post-hoc pairwise comparison tests were carried out with a Bonferonni adjustment for multiple comparisons.

Results

Descriptive statistics for both dominance interactions and cache placement for each of the marked squirrels are presented in Table 9. As can be seen from the table there is a skew to the both the caching and social rank data; one squirrel (End Half of Tail, adult male) dominated the provisioned food over most of the observation periods and was responsible for most of the chases/displacements made (161/183) as well as most of the caches (85/303) in comparison to other individual squirrels. Throughout observations all 100 of the provisioned nuts were taken by squirrels within an average of 1h 14m.

Table 9. *Descriptive statistics for each of the marked squirrels observed in social interactions and caching. We observed a total of 303 caches being made, 184 of these by marked squirrels, and 183 chases involving a marked squirrel. Eighty per-cent of the caches made were provisioned hazelnuts and squirrels identified as male, female, juvenile or adult appeared to cache similarly (excluding End Half of Tail).*

Rank (Landau's index of linearity)	Squirrel ID	Chases made and won (out-degree)	Chases received and lost (in-degree)	Number of squirrels dominant to	Sex	Age	Total number of caches made	Total number of hazelnuts cached	Average number of curtailed digs made (SD)	Average caching distance from stump (SD)	Average caching distance from nearest neighbour (SD)	Average caching distance from cover (SD)
1	End Half of Tail	161	3	7	M	Adult	85	80	0.82 (1.42)	9.07 (4.55)	10.69 (4.91)	2.52 (1.81)
2	Hip Band	6	0	3	F	Adult	17	5	0.29 (0.59)	10.57 (5.03)	-	1.96 (1.95)
2	Tip & Base of Tail	3	22	3	F	Adult	3	2	2.00 (2.65)	20.30 (4.50)	-	1.90 (0.92)
3	Spine Stripe	3	89	2	M	Adult	38	28	0.95 (1.16)	13.34 (5.71)	13.14 (6.88)	3.05 (1.90)
4	Back Spot	1	4	1	F	Adult	4	1	4.00 (1.16)	20.25 (11.24)	6.90 (4.67)	2.25 (2.33)
4	Bum Spot	5	20	1	M	Adult	6	5	1.50 (1.05)	16.44 (6.84)	10.02 (8.14)	1.56 (1.19)
4	Open Circle Back	1	4	1	M	Adult	3	3	2.00 (1.00)	12.10 (2.43)	-	4.10 (2.79)
5	Neck Spot	1	8	0	F	Adult	2	1	2.00 (2.83)	9.30 (2.55)	14.40 (9.33)	3.00 (2.55)
5	Side Crosses	2	33	0	M	Juvenile	17	15	1.12 (1.78)	11.38 (6.26)	12.90 (5.88)	2.05 (1.60)
-	Belly Band	0	0	0	F	Adult	1	0	0	24.6 (12.18)	11 (7.08)	0.60 (1.12)
-	Base of Tail Ring	0	0	0	F	Adult	8	5	1.62 (1.41)	11.78 (3.61)	-	3.11 (1.85)
-	Racing stripes	0	0	0	F	Adult	0	0	-	-	-	-
-	Three Spot	0	0	0	M	Juvenile	0	0	-	-	-	-
-	Unmarked	-	-	-	-	-	119	96	-	-	-	-

Dominance interactions

A dyadic interaction dominance matrix was used to generate an ordinal dominance hierarchy based on chases/displacements made and won versus those received and lost for the marked squirrels that were observed in interactions at the provisioned food. This was calculated as per the method of Brown (1975) to better control for treatment of reversals and intransitivity in the data. This is presented in an interaction matrix (Figure 18), which shows the identity of individuals making and receiving most chases/displacements, and reflects the best order of dominance in the group.

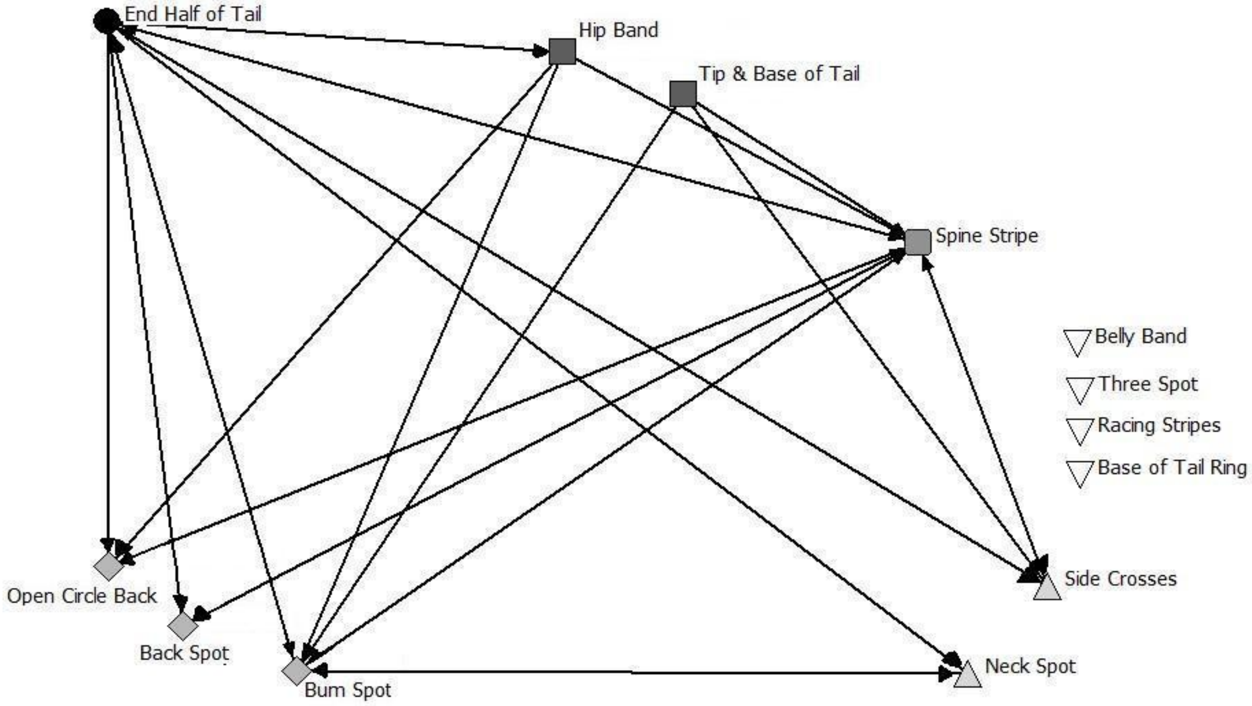


Figure 18. Dominance network of the marked squirrels based on interactions at a food source. Calculated using the method of Brown (1975) and generated using UCI NET; those relationships represented as equal ranks come from Landau's V_a = 1 + 0.5 formula. The squirrel denoted by the black circle node initiated and won the most chases/displacements (but also lost three interactions) and also was dominant over the most squirrels, followed by squirrels represented by the dark grey square nodes who were each dominant over three squirrels, the soft edge medium grey node represents a squirrel that was dominant to two squirrels, and the squirrels represented by the grey diamonds were each dominant to one squirrel. The grey upward triangle nodes depict squirrels that were always only the recipient of a chase/displacement. Four squirrels (white inverted triangles) were not involved in any interactions but were observed at the provisioned food when there were other squirrels present.

We used Landau’s index of linearity (in Lehner 1996; equivalent to the method of Kendall 1948) to assess whether the dominance network was a linear hierarchy, which allowed ranking of squirrels based upon the number of individuals subordinate to them (Table 8). The index (*h*) is calculated to the following formula:

Linearity was calculated using $V_a = 1 + 0.5$ for individuals of equal rank where V represents the number of animals that individual ‘*a*’ dominates. A low value of for the degree of linearity was attained, *h* = 10.2. This non-linear relationship is likely due to several squirrels in the hierarchy having attained equal ranks, and because most interactions were made by one squirrel dominating all others at the provisioned food patch. Thus, the food competition dominance network reflects more of a tyrannical or despotic structure.

Cache placement and dominance rank

Data for caching distances based upon individual identity are presented in Table 9, which do not reveal any striking differences between the tyrant squirrel and its subordinates. Therefore, we used Landau’s index of dominance rank to explore whether there was a difference in caching distances, as opposed to individual identity. As the data were skewed because one squirrel dominated the provisioned food patch, this could have limited the amount of food that other squirrels in the vicinity could sequester. Therefore we used non-parametric analyses that were not sensitive to violations of normality. We compared if there were differences in the following measures according to relative dominance rank: caching distance from provisioned food, caching distance from cover, caching distance from nearest neighbour. Overall the squirrels tended to place caches an average of 11.71m (SD = 6.01) away from the food source, 11.58m (SD = 6.06) from their nearest neighbour, and 2.61m (SD = 1.82) from cover (data for caching distances based upon individual identity are presented in

Table 9). A Kruskall-Wallis analysis revealed no significant differences for any of the measures (*p* > .05) based upon dominance rank.

Cache placement and pilferage reduction strategies

In order to examine whether pilferage avoidance behaviours were displayed as a function of caching distance to different areas of risk three GZLMs were carried out. These measured whether different pilferage avoidance strategies (caching orientation, curtailed digging, and use of visual barrier) were used differentially as depending upon caching distances to areas high in pilferage risk, competition and predation risk. A summary of their outcome is presented in Appendix C.

For the number of curtailed digs made, a GZLM was carried out based upon a Gamma probability distribution with an Identity Link Function. The minimum adequate model was significant, AIC =214.25, X^2 (24) = 5.41, $p < .001$. The best predictors for explaining the variance in the number of curtailed digs made was the caching distance from their nearest on-looking squirrel X^2 (22) = 5.31, $p < .001$, and the caching distance from the food source X^2 (21) = 69.23, $p < .001$. The number of curtailed digs that were made was significantly affected by caching distance to the nearest on-looking squirrel and caching distance from the food source, so that the number of curtailed digs increased as caches were placed farther away from conspecifics and farther away from the provisioned food source. These results are presented in Figure 19.

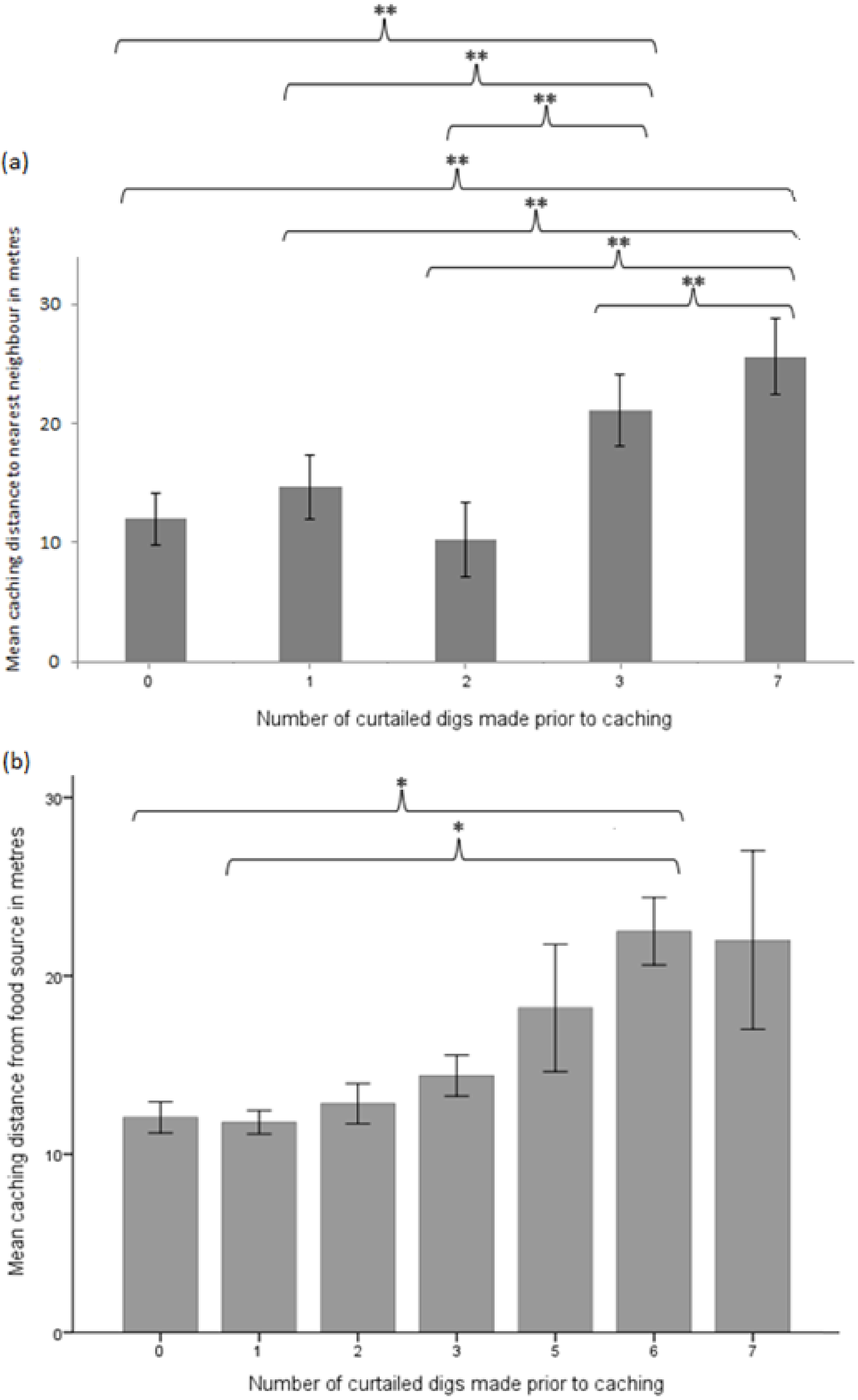


Figure 19. Result of GZLM follow-up tests for number of curtailed digs made as a function of (a) caching distance to nearest squirrel, and (b) caching distance to the provisioned food. Error bars represent ± 1 standard error. * $p < .05$, ** $p < .001$.

For caching orientation to nearest neighbour, a GZLM was carried out based upon a binary logistic probability distribution. The minimum adequate model was significant, AIC =206.45, X^2 (72) = 78.73, p = .001. The best predictor for explaining the variance in the number of curtailed digs made was the caching distance from their nearest on-looking squirrel X^2 (26) = 12.81, p < .009. Squirrels would be more likely to orientate themselves away from the nearest onlooking neighbour when they were farther away from them, displayed in Figure 20. No other factors were significant in the optimal model.

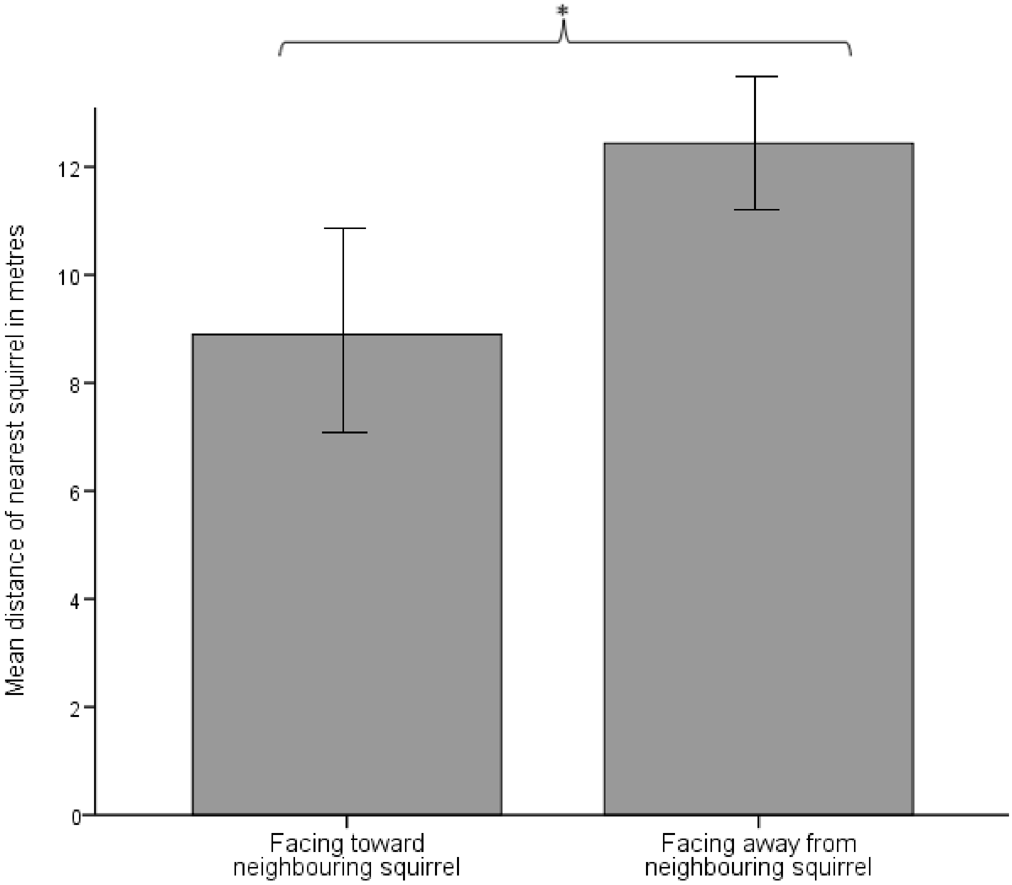


Figure 20. Results of GZLM follow-up tests for caching orientation to nearest neighbour as a function of distance to nearest neighbour. Error bars represent ± 1 standard error. * p < .05.

A GZLM was carried out based upon a binary logistic probability distribution to determine whether subjects were more likely to use a visual barrier while caching in the presence of another squirrel. Use of a visual barrier did not vary as a result of any of the cache placement distances included in the full model, AIC =200.72, X^2 (74) = 69.22, p = .107.

Discussion

To determine whether dominant and subordinate squirrels behaved differently when foraging and caching, we first examined social structure within our subjects. It was found that one squirrel (End Half of Tail: an adult male) was responsible for the majority of caches made and won more dominance interactions than any other squirrel. However, the nature of the social hierarchy was tyrannical which contrasted with our expectations of a linear hierarchy. As a function of dominance rank cache placement was also measured in terms of distance to the food source, other squirrels and refuge. We found that there were no differences in these measures based upon dominance rank.

We then compared whether there were differences in use of pilferage reduction behaviour as a function of cache placement. In terms of using a visual barrier between themselves and the nearest conspecific, there was no effect of cache placement.

In terms of caching orientation to the nearest conspecific, squirrels would be more likely to orientate themselves away from their nearest neighbour when they cached farther away from them, and orient toward them when placing caches close to them. This finding lends support for a competition-avoidance hypothesis and indicates that squirrels might be acting in ways to visually monitor potential competitors, which may minimise the possibility of an agonistic encounter. However, it is also possible that in locations where there is a higher density of squirrels, that individuals are more likely to face toward another squirrel.

Finally in terms of caching distance to the nearest neighbour, squirrels made more curtailed digs when they cached farther away from a conspecific and farther away from the food source. This is opposed to what we would expect from an individual minimising their pilferage risks, and thus we can reject our pilferage-avoidance hypothesis. It is possible that when caching close to a conspecific or at a location where the density of foraging competitors is high (i.e. a food source), an onlooker could pose a more immediate risk of competition to the cacher by supplanting or chasing the caching individual. Thus engaging in curtailed digging could be risky to the cacher in locations where there is high foraging competition or when conspecifics are close by. This could suggest once again squirrels are acting in ways to avoid competitive interactions.

Dominance hierarchy in the grey squirrel and its effect on caching

As an underlying basis for this study, we aimed to quantify a linear dominance hierarchy previously reported in grey squirrels so that we could explore its effects on their food hoarding behaviour. However, the dominance hierarchy we found was notably different from what we expected. Previous studies report that grey squirrels have a transitive linear dominance hierarchy, where a number of higher ranking adult males dominate younger subordinate males and females (Allen & Aspey 1986; Flyger 1955; 1960; Horwich 1972; Koprowski 1996; Pack et al. 1967; Taylor 1966; Thompson 1978). While we found that the most dominant squirrel in our population was an adult and male as expected, the nature of the dominance network in the current study did not reveal what had been previously found with grey squirrels. This produced unexpected, but nevertheless interesting, effects on the rest of our behavioural measures.

After calculating dominance rank within our population, our study aimed to explore whether individuals of different status made different cache placement decisions. Despite having one clear high ranking individual within our population, no differences in cache placement were found between the different dominance ranks. Again, this finding is not what we expected to find. While this has not been studied in grey squirrels, the literature on food storing rodents and birds shows that dominance plays a an important role in food hoarding behaviour in terms of where to forage (Hogstad 1988), when (Burns & Steer 2006) and where to cache (Shaw & Clayton 2012a), and how to protect stores (Bugnyar & Heinrich 2005; Bugnyar & Kotrschal 2002; Goodwin 1956; Dally 2004; Dally et al. 2005a; Jenkins & Breck 1998). However, given the dominance network that was found in the current study, with one individual monopolising resources, it is doubtful whether there would be individual differences in caching strategies among subordinates who had limited access to the provisioned food source.

There are methodological reasons that could have contributed toward the current results. The provisioning methodology used here has the advantage of increasing the number of caches observed during a limited study period and thus can greatly increase volume of data. While some studies scatter the provisioned food rather than positioning in one location we chose not to do this so that we could observe food competition to determine dominance structure. However, presenting a large regular supply of food to a population of squirrels creates an artificial bonanza situation that could have affected the natural dynamics of the population network. This could be particularly problematic if the provisioned source is placed at the centre of one individual’s home range but where other squirrels also forage. In the current study this might had led to the formation of a tyranny where one would not normally exist. An alternative way to run this type of study would be to conduct observations of caching whilst naturally foraging (as opposed to a provisioning), but use a provisioning station at different locations and at separate times around the observation site to study dominance interactions. This might help to provide a more natural competitive situation, and reveal any changes in dominance hierarchy as provisioning is moved across the site. However, for studies that are limited to monitoring behaviour during peak caching times it might provide limited data, with too few caches observed for trends to be determined.

Looking more closely at the previous studies conducted, their individual methodology varies considerably. For instance, Allen and Aspey (1986) measured competition for access to a food bucket in a group of wild-caught squirrels placed in an enclosed arena, while Thompson (1977) and Koprowski (1966) simply monitored natural occurrences of aggression in free-ranging individuals that were not even necessarily engaged in foraging. Despite using different ways to measure dominance, across these studies linear hierarchies are consistently reported. The current study used a methodology that was similar to Pack et al. (1967). In their study they monitored the natural occurrences of dominance interactions of marked individuals at a provisioned feeding station. As in the current study, dominance was assessed in terms of displacements and chases by a dominant toward at subordinate which prevented access to the provisioned food. Similarly, adult males were responsible for the majority of these. At one of their sites, even with a relatively low sample size (similar to the current study) of 19 individual squirrels they reported a “straight line hierarchy” (p. 723).

If methodological differences between studies (for example, in food provisioning, the size of the site or population) do not provide a full explanation of why the current data are so different from previous results, perhaps the social environment could offer an interpretation. Indeed it is likely that the data from one rogue squirrel has contributed to this outcome; this individual might simply not have been representative of how squirrels behave. However, because this one individual had such an impact upon the rest of the study population at the experimental site, it is impossible to determine how the social network would have been different without this one squirrel, whether it would be linear, or whether simply another squirrel would take over its rank.

Cache placement in relation to competition, pilferage and predation

Although the dominance data were not as expected, we were still able to explore pilferage avoidance behaviour in relation to the cache placement decisions of our sample population. This was done in terms of how far they cached food from its source where there was likely to be a high risk of competition, how far they cached from their nearest onlooking neighbour, and how far they cached from refuge. Generally squirrels appeared to act in ways that were associated with sensitivity to risk of competition rather than pilferage. Cachers were more likely to face conspecifics when they cached closer to them and were less likely to make curtailed digs in the close proximity of conspecifics. These results support the research of Hopewell et al. (2008) who report that, at a food patch, grey squirrels respond to conspecifics primarily as competitors rather than potential pilferers. Given the nature of the dominance network in the current study, the benefits of monitoring the behaviour of competitors (rather than facing away to cache, or caching behind a visual barrier) are clear; an aggressive squirrel was monopolising food supplies and all others needed to monitor this individuals behaviour.

Our current data do not lend any support to the pilferage avoidance literature. A number of caching birds and mammals have been reported to engage in behaviour while caching that serves to limit visual information about the location of stores. For instance, when being observed caching some species have been shown to place caches behind visual barriers (Bugnyar & Kotrschal 2002), face away from conspecifics (Leaver et al. 2007), store in more shaded locations (Dally et al. 2004), and in more out-of-sight locations (Dally et al. 2005b; Heinrich & Pepper 1998; Pravosudov 2008; Steele et al. 2008) compared to when are not being observed. From these results one would predict that a cacher in the current study would be more likely orient away from onlookers to conceal information about their cache, whereas the opposite was reported in the current data. In addition to this, Hopewell and Leaver (2008) found that grey squirrels made more curtailed digs in the presence of conspecifics compared to when caching alone, but in the current study we found they made fewer curtailed digs when they were closer to another squirrel. However, there are several methodological reasons why our current results cannot be directly compared with those from previously studies, particularly design and population structure differences.

As already discussed, the current study used provisioning, which creates an exaggerated competitive situation. Even though there is more than enough food available, because the food is presented as a bonanza rather than a foraging patch, the competition to cache is intensified. At a time of year when caching rates are already at their peak, the provisioned food encourages an accelerated rate of caching compared to what they would be naturally, with individuals attempting to sequester and store as much food as possible before the bonanza is depleted. Provisioned nuts were taken by squirrels within 1-2 hours, with the majority of these taken out of sight and stored or eaten before the same individual returned to repeat the behaviour. Given this urgency to cache, and such an abundant supply of food, it could be argued that the motivation to engage in pilferage-reduction behaviour is reduced, with the pressure of competing with others at the same provisioned patch being made much more immediate.

Another possible reason why we did not find support for ourpilferage avoidance hypothesis as we expected may be because studies that report these behaviours do not tend to take measurements of cache placement (i.e., in terms of distance from the food source, neighbour or refuge) as a function of whether pilferage avoidance was displayed (e.g., Leaver et al. 2007). Typically cache distribution is recorded or behaviour is measured as present or absent, as opposed to being recorded as a function of distance from locations varying in risk as it was in the current study. In addition, studies that do link pilferage avoidance to dominance tend to be conducted on species that are known to demonstrate a clear dominance network (e.g., Eurasian jay: Shaw & Clayton 2012a). Given that the dominance hierarchy in the current study was so different from what would be expected from previous studies, it makes the results relating to cache placement behaviour difficult to generalise to other populations of squirrels.

Finally, we also expected to find a difference in pilferage reduction behaviour in terms of willingness to incur predation risk while caching. This was not found, so the current study was not able to further understanding of how predation risk might be traded-off against other risks, such as pilferage. Though this kind of trade-off has been studied in other food hoarding species, our knowledge of it in squirrels is limited, with only one study reporting that they may trade-off predation with pilferage in their placement decisions (Steele et al. 2014). Further research on grey squirrels cache placement behaviour would provide a great contribution to this topic and increase our understanding of how squirrels are deciding where to cache; it could also help to clarify how squirrels decide where to pilfer as this is something that is still unclear (discussed in Chapter 5).

There are several possible reasons why no differences in caching distance to refuge were observed in our current study. It is possible that the measure of predation risk was not sensitive enough to detect differences in behaviour. The study site was selected because it was known as having had a large population of grey squirrels for a number of years. However, this location also had substantial canopy cover (60-80% throughout the study) and provided extensive areas of refuge from both terrestrial and aerial predators (hence its thriving population of squirrels). Therefore the risk of predation may not have been substantial in this location, particularly when the more immediate threat of competition was so high from one dominant squirrel. Though many studies do use distance to refuge as a measure of predation risk (e.g., Brown et al. 1992;

Bowers et al. 1993; Ekman 1987; Lahti et al. 1998; Newman et al. 1988), often measuring or simulating direct cues of predation risk, such as visual or auditory cues, can provide a more direct measure of behaviour in response to these cues. Rather than providing a degree of risk, this enables the experimenter to monitor differences in behaviour (for example, cache placement) when the cue is present versus when it is absent. In environments where competition is high, such as during peak caching season, or those that have abundant canopy cover, which is typical for grey squirrels, exploring behaviour in this way would help to distinguish behaviours that are in response to competition from those that are in response to perceived predation risk (discussed in Chapter 6).

Conclusion

This study has reported a more exaggerated dominance network than grey squirrels were previously thought to have, and social dominance was not found to affect cache placement in a similar manner to food storing birds. Squirrels in the current study appeared to engage in behaviour that allowed them to more easily respond to a competitive behaviour, including: orienting themselves toward and engaging in less curtailed digging while caching in proximity to conspecifics. Our measure of predation risk was not found to influence behaviour in any way. Because of the unexpected findings several methodological concerns have been outlined that could have contributed to the outcome of the study. It is suggested that future exploration of these topics investigate them in a different manner; some suggestions have been outlined, and alternative field methods are presented in Chapters 5 and 6.

Chapter 5: Factors affecting cache pilferage rates at landmarks: predation risk and food availability.

Introduction

The ability to locate and recover their stores can influence scatter hoarders decisions about where they make their caches. Spatial information and visual landmarks have been reported to be used by a number of food hoarding species, including grey squirrels, to act as beacons during caching and recovery of their stores. Caching species also pilfer the caches of others while foraging, though the precise mechanisms they use to achieve this are unclear among the Paridae and Rodentia. The problem of pilferage has been examined extensively across a range of species from the point of view of the cacher (reviewed in Chapter 2), however few studies, beyond the OSM literature, have investigated the behaviour of pilferers. Given that cachers use visual cues to aid memory for their stores, the current study addresses whether landmarks might act as a beacon to aid pilferers by cuing the location of caches.

Cues used during caching and recovery

Food storing Corvidae and Paridae appear to be careful where they place their caches. Field and captive studies show that the use of spatial information (discussed in Feenders & Smulders 2011 and Vander Wall 1989) and local cues (“beacons”) can play a strong role in food caching and may be used to aid recovery. For instance, some birds demonstrate a preference to cache close to landmarks (black-capped chickadee: Herz et al. 1994; Clark's nutcracker: Vander Wall, 1982; Kamil, Balda & Olson 1994; Balda & Turek 1984; magpie: Feenders & Smulders 2011; Western scrub jay: Watanabe 2005), show site preferences that enhance retrieval accuracy (Male & Smulders 2007a), and have difficulty recovering food when visual cues have been moved or removed (black-capped chickadee: Brodbeck 1994; Cheng & Sherry 1992; Duff et al.1998; Clark's nutcracker; Gould-Beierle & Kamil 1996).

Some scatter hoarding mammals also appear to use visual cues from their environment when they cache food, and are better at recovering their stores when landmarks are intact (Merriam’s kangaroo rat: Barkley & Jacobs 1998; Mongolian gerbil: Collett et al. 1985; Southern flying squirrel: Gibbs et al. 2007; laboratory rat: Olton & Samuelson 1976; yellow pine chipmunk: Vander Wall 1991; Vander Wall et al. 2006). However, cache recovery in mammalian scatter hoarders differs from birds because they can more heavily rely on olfactory cues to locate their stores. Nevertheless, when comparing the use of spatial and visual cues with olfactory information, cachers appear to benefit more from spatial and visual cues to locate their stores compared to those using random olfactory search (Merriam’s kangaroo rat: Jacobs 1992b; pine chipmunk: Vander Wall 1991, 2000; deer mouse: Vander Wall 2000; for reviews of rodents and other mammals using memory to recover caches also see: Smith & Reichman 1984; Smulders et al. 2010; Sherry 1985). These studies demonstrate that landmarks can act as visual cues and can have a critical role upon caching decisions and recovery success in a variety of scatter hoarding species.

Cues used during caching and recovery in the Eastern grey squirrel

Remembering the location of buried caches, as opposed to simply relying on olfaction, should be critical for the survival of scatter hoarding grey squirrels. This species is active all winter in climates that are frequently under snow for several weeks, if not months, making it more difficult for caches to be recovered by olfactory cues alone (Lewis 1980). It is estimated that grey squirrels store around 3000 caches per season (Macdonald 1996), placing individual nuts and seeds in separate cache sites, and recovering them anywhere up to several months later (Thompson & Thompson 1980).

Experimental studies show that grey squirrels demonstrate proficient cache recovery. They have been found to be better at recovering their own caches than those they have not seen buried by others (Jacobs & Liman 1991). Jacobs and Liman suggest that squirrels will return to locations where they have buried nuts using visual cues, but then search for the precise location by the odour of the cache contents. Macdonald (1997) demonstrated that wild squirrels remembered the precise locations of artificial caches using visual cues, and suggests that the memory of grey squirrels is accurate enough to use in cache recovery. Moreover, even though squirrels possess powerful olfactory capabilities (Lewis 1980), McQuade et al. (1986) found that grey squirrels prefer to use visual and spatial cues over olfactory cues to recover experimenter-made caches. McQuade et al. trained wild-caught squirrels to associate three different and distinct cues with a seed reward contained in a petri dish: olfactory cues (flower extracts on the covers of the petri dish), visual cues (coloured tape covering the dish), and spatial cues (a 3x4 spatial arrangement of the dishes around the arena). The researchers found that squirrels were able to successfully recover caches using all types of cue after a delay of 1-2 days, but when provided the opportunity to recover from all types of cue simultaneously, squirrels showed a preference in which type of cue they would use. Squirrels preferred to use visual cues the most when locating hidden food, then spatial cues, and least of all used olfactory cues. McQuade et al. even found that when seeds were removed from the petri dishes squirrels would continue to follow cues in this order of preference when they were no longer associated with a reward. This study shows how extrinsic information (visual and spatial cues) is preferred over olfactory information during recovery of artificial caches, but also demonstrates how these cues could enhance cache recovery.

Cache pilferage in the Eastern grey squirrel

It is interesting among the cache-recovery literature, that subjects frequently recover items that they had not made themselves. Pilfering behaviour is widespread among food storing species, particularly those that scatter cache. Within several species of Corvidae pilfering behaviour has been attributed to the use of OSM, though there is little evidence for this among Paridae and Rodentia, or indeed squirrels (reviewed and experimentally tested in Chapter 3). Many scatter cacher species reside within dominance structured groups, and thus being more dominant can also help in accessing caches if they are pilfered immediately (reviewed in Chapter 4). However, what of the pilfered nuts which have not been observed being buried? Given that squirrels show a preference for using visual cues to store food, it is possible that food thieves might use visual cues to direct their pilfering efforts.

In order to explore this it is important to consider what type of landmark or environmental feature might serve as a beacon to a caching squirrel. In the studies mentioned above small man-made visual cues were provisioned to captive (coloured cinder blocks: Jacobs & Liman 1991; coloured petri dishes: McQuade et al. 1986) and wild subjects (poles with coloured signs: Macdonald 1997). This may be problematic firstly because these items do not necessarily represent the types of feature that a squirrel would encounter in its natural habitat, and secondly, because the visual cues were impermanent and removable this makes them more unpredictable features within these squirrels' landscapes to rely on to recover caches. For naturally foraging grey squirrels, the most useful visual cues are likely to be trees, shrubs, rocks and other permanent landscape features that remain constant throughout the year; urban squirrels may rely on man-made fixtures as well. Therefore, in order to explore the type of visual cue that squirrels might use to cache and aid pilferage, it is important to consider features that are regularly encountered by foraging wild grey squirrels.

A number of studies show that artificial caches made closer to the base of trees are stolen at higher rates. To measure pilferage risk in relation to cache placement, Leaver et al. (2014) carried out a field study that buried hazelnuts at varying distances to trees and in different spaced clusters. It was found that nuts buried closer to the base of trees were at a higher risk of being stolen, as well as those that were placed close to other caches, compared to those in wider distributions and farther away from the tree. This study supports previous research that caches spaced more widely are less vulnerable to pilferage (e.g., Leaver 2004; Male & Smulders 2007b; 2008), and more recently that trees are a source of pilferage (Steele et al. 2014). However, these findings do not provide any indication of why caches closer to the base of trees may be more vulnerable to pilferage.

It is possible that caches are more vulnerable to pilferage under trees because the tree acts as a beacon to both cachers and pilferers of the whereabouts of hoarded food. However, it is also possible that because squirrels spend more time foraging under the cover of trees, they happen upon caches more often in these locations. It has been suggested that survival rates of caches are lower near a food source because they are pilfered more extensively by naïve competitors that visit the location more frequently than other areas of vegetation (Brodin, 1993; Clark & Clark 1984; Janzen 1970; Tamura 1998; 1999; Tamura, Hashimoto & Hayashi 1999). Alternatively, Stapanian and Smith (1978; 1986) and Steele et al. (2014) suggest that caches closer to cover are more likely to be pilfered because there is lower risk of predation for opportunistic cache-pilferers to forage in these locations. Thus, the reason that caches are stolen at a higher rate when stored closer to the base of trees is unclear; because it is safer to forage closer to a potential escape route, because there is generally more food available under the cover of trees, because the density of caches is higher under trees and so attracts pilferers as a source of food, or indeed some combination of these factors. The goal of the current study is to investigate this experimentally from the point of view of the pilfering animal in order to determine whether pilferage rates differ depending upon predation risk or food availability. This will also help to provide insight into whether pilferers target trees as beacons for caches specifically or whether other types of landmark are pilfered from equally.

Pilferage rates at trees: predation risk and food availability

The current study was conducted to examine the pilferage behaviours of wild squirrels. Artificial caches were buried around landmarks that were permanent features of the landscape and could act as visual cues to indicate the location of caches. In order to ascertain whether trees were pilfered from more because they provided an escape route or acted as a source of food, we buried artificial caches around naturally food-bearing trees (that provide nuts and seeds during the autumn months), non-food bearing trees (that do not provide any source of food to a caching squirrel other than leaves and bark) and manmade landmarks (lampposts and signposts) that were difficult for squirrels to climb, provided no overhead cover, and were not close to natural sources of food. In addition, half of these manmade landmarks were also provisioned with food to investigate if pilferers were simply attracted to profitable sources of food, regardless of their location. Because the caching activity of grey squirrels is highly seasonal, peaking in mid to late autumn (Thompson & Thompson, 1980) we monitored pilferage rates at these four types of landmarks across two seasons: autumn (where there is an abundant food supply and high level of caching among squirrels) and spring (where there is a low natural food supply, and squirrels are reliant upon recovering their caches for food).

We made two contrasting predictions about the type of strategy that might be used by pilferers, and one prediction based upon seasonal difference in pilferage: (1) If pilferers were primarily choosing their foraging locations in order to avoid predation risk, pilferage rates would be highest at the food-bearing and non-food bearing trees, which provide safety from predation. (2) If pilferers chance upon caches opportunistically while foraging near profitable food sources, then pilferage rates should be highest at the food-bearing trees and food-bearing lamp/sign-posts. (3) Caches should be at greater risk from pilferers in the spring when nut availability is low compared to the autumn, when food is abundant.

Method

Authorisations

This study was carried out in accordance with the Association of Animal Behaviour Guidelines for the Use of Animals in Research (2012), the University of Exeter Psychology Ethics Committee, and with permission of the University of Exeter Director of Grounds.

Population

Pilferage rates of artificial caches were monitored across 15 sites (N = 15) on the University of Exeter Streatham Campus. The campus flora comprises a wide variety of species across 113 hectares of botanical gardens, parkland and woodland and so provided an ideal location for this study. The sites were a minimum of 250m apart from one another to avoid overlapping home ranges between individuals (monitored using Free GPS iPhone application by Code Burners and verified by www.itouchmap.com). Previous research has reported that the maximum known linear measure of home range size for a grey squirrel is 136.7 metres (Doebel & Mc Ginnes 1974), a measure which has been used for similar purposes in recent grey squirrel studies (e.g., Getschow, Rivers, Sternman, Lumpkin & Tarvin 2013); and the maximum known distance a squirrel will travel for food from its nest is approximately 220m (Jacobs 1989). Therefore there is a good degree of certainty that the sites sampled the pilferage behaviour of different squirrels.

Verifying target population

We monitored the pilferage activity at the sites for the duration of the study in order to verify that we were indeed measuring pilferage by squirrels rather than sympatric corvids who forage on the same resources as the resident squirrels, and have been observed to pilfer the freshly made caches of squirrels (Vernelli 2013), and have been reported to use their cognitive abilities to help them steal caches as opposed to smell (discussed in Shettleworth 1990). Throughout the testing days at each site we also monitored squirrel activity. At 48 hour intervals a 10 minute observation session took place to ensure there were still squirrels present. If during this observation period at least one squirrel had not been observed anywhere at the site, the site would have been excluded from the study (in no cases was this necessary). Furthermore, on days when we buried artificial caches, sites were monitored from approximately a 20m distance for 30 minutes immediately after burial to ensure that corvid onlookers did not retrieve any of the caches, and to monitor any immediate pilferage by squirrels. In addition, on days when caches were checked for pilferage, sites were monitored for any visual signs of other species that might be visiting the sites, such as footprints, fur, or faeces. On several of these occasions squirrels were witnessed pilfering the artificial caches (once unexpectedly recorded on a video-camera phone), and wild rabbits were present at intact caches but were uninterested in the caches or provisioned food. The only evidence of excavating and eating the artificial caches matched what would be expected from squirrels extracting their contents (see Jacobs 1989 and references therein).

Design

This study comprised a 2x2x2 repeated measured design where each of the 15 sites acted as a subject. Each site contained four landmarks that could act as beacons for food storing squirrels and thus also for pilferers. We examined the main effect of predation risk (mature tree versus lamp/sign-post) and the main effect food availability (food-bearing/provisioned versus non-food-bearing/non-provisioned) on pilferage rates, across two seasons (non-independent observations n = 30); with the 4 types of landmark tested in autumn 2012 at each site, and 4 different landmarks tested in spring 2013 at the same sites.

The landmarks were within approximately 20m of one another, and were selected for their similarity in that they had a minimum of 1m grass circumference, and were at similar distances from roads, paths, buildings, and without any additional sources of refuge within the vicinity (i.e. overhanging neighbouring tree canopy). The tree landmarks were always mature so that they could provide a suitable escape / cover from a predator for a squirrel. The food-bearing trees were species that provided seeds that squirrels were known to consume and cache, including 7x beech (*Fagus spp*.), 8x chestnut (*Aesculus spp*.) and 15x oak (*Quercus spp*) trees. The non-food trees simply provided refuge to a squirrel but were not a source of food, including ash 5x (*Fraxinus spp*.), 8x birch (*Betula spp*.), 6x English lime (*Tilia spp*.), 7x maple (*Acer spp*.),2x willow (*Salix spp*.), and 2x palm (*Arecaceae spp.*) trees. For the man-made landmarks we selected a series of signposts and lampposts that were 1-3m in height as these acted as a potential beacon but could not offer cover from an aerial predator, or a means of escape from a terrestrial predator. So that foraging individuals would learn that the food-bearing lamp/sign-post landmarks were a source of food, they were provisioned with 30 acorns (origin *Quercus spp*.) on day 1 of testing (in both the autumn and spring testing seasons), and topped up on days 3 and 5 if any had been eaten (at least 10 nuts had always been eaten), so that there was always a maximum of 30 nuts (discussed in Table 10). Note that the acorns used to provision were collected from non-test locations; acorns were always used to provision because of their greater availability at these non-test sites compared to other types of nut.

Procedure

The study was carried out over 20 consecutive days for each landmark, and all four landmarks at each site were tested during the same 20 day period, but not all sites were tested at the same time (3 sites in September, 6 sites in October, and 6 sites in November 2012; with corresponding order for March, April, May 2013). Procedures for each site are listed in Table 10, illustrations of the distributions of the artificial caches are presented in Figure 21, and the structure of the artificial cache is presented in Figure 22.

Table 10. *Study procedures. The study took place between 10am and 4pm over a 20 day period for each of the sites and landmarks. Note that all natural and provisioned material at the sites were handled using latex gloves.*

Day		**Activity**
1	-	One of each of the four landmark types were selected at each site that was being tested.
	-	Quadrat measurements were taken (average of three 25cm^2 measures) within 1m of each landmark to monitor current food availability (if non-food bearing landmarks had any food items within their circumference an alternative landmark was selected).
	-	One of the lamp/sign-posts landmarks was randomly selected to act as food-bearing, and 30 acorns (origin *Quercus spp.*) were scattered on the ground within a 1m radius of its base.
3	-	Quadrat measures were taken, and any acorns that had been removed from the provisioned lamp/sign-posts were replenished (so that there was always a maximum of 30).
5	-	As per day 3.
7	-	At a 1m (± 20cm) radius around each landmark ten caches were made, each containing one single hazelnut (with shell), placed at equal 1m (± 20cm) distance from one another. To make this cache a hole was excavated 5cm into the soil using a metal teaspoon, a hazelnut was pressed into the hole, a pinch of green unscented fish tank gravel was placed on top of the nut, and the site was recovered with soil and leaf litter so that the ground and surrounding area looked undisturbed.

8	-	Sites were visited to record the number and location of caches pilfered.
9	-	Sites were visited to record the number and location of caches pilfered.
10	-	Sites were visited to record the number and location of caches pilfered.
11	-	Sites were visited to record the number and location of caches pilfered.
14	-	Sites were visited to record the number and location of caches pilfered.
17	-	Sites were visited to record the number and location of caches pilfered.
20	-	Sites were visited to record the number and location of caches that had been removed. All remaining caches and gravel were removed from the sites.

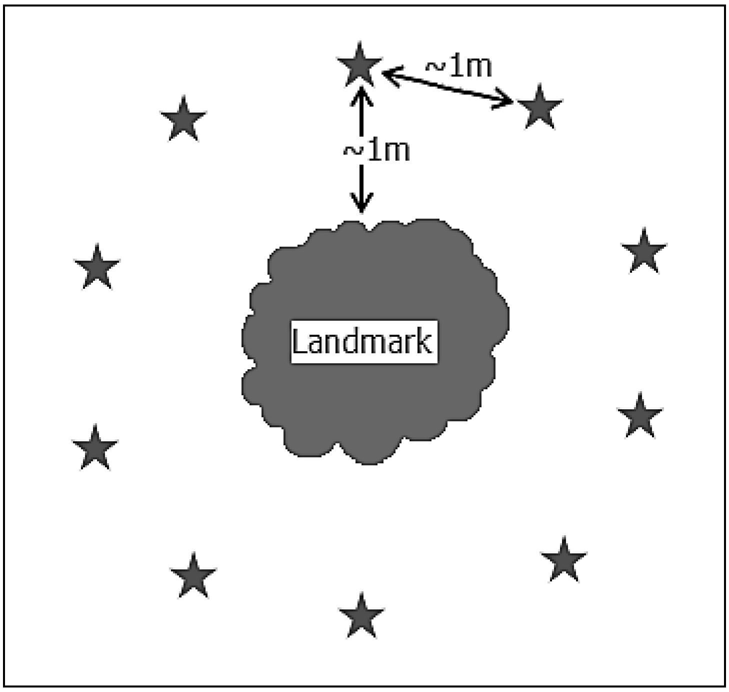


Figure 21. Example of cache distribution around a landmark. Stars represent caches placed at approximate 1m distances from one another and the landmark.

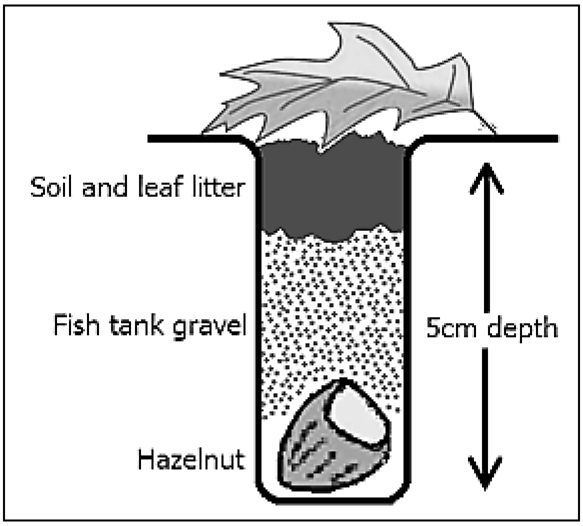


Figure 22. Illustration of the composition of each cache. The fish tank gravel was used so that it was easily visible to the experimenter when scattered around the excavated cache after the nut had been removed. This method has been successfully used in previous field research (Leaver et al. 2014). Hazelnuts were chosen because they have been favoured in previous captive and field food-preference tests which is likely due to their slow perishability and high nutritional value.

Analysis

We analysed two measures: (1) pilferage levels in terms of whether landmarks experienced total-, some-, or no pilferage, and (2) the number of items stolen at different time intervals, namely the first three days after caches were buried versus the last three days that caches were buried. Models reported are 2x2x2 factorial designs that examine the main effects of predation risk (tree versus lamp/sign-post), the main effects of food availability (food-bearing versus non-food bearing), and the main effects of season (autumn versus spring), and two-way interactions between these variables.

These data were not normally distributed, and therefore we opted to perform GEEs which accommodate this and our small sample size for the same reasons as outlined in Chapter 2 of this thesis. GEE’s were carried out using a ordinal regression with a cumulative logit link function, with an independent correlation structure. Follow-up comparison contrasts tests were carried out with a Bonferroni adjustment for multiple comparisons.

To compare whether there were differences in the proportion of caches pilfered in the first three days after burying compared to the last three days we carried out a repeated measures t-test. To compare whether pilferage varied between the conditions over the first three days and last three days we used a 2x2x2 repeated measures ANOVA; this examined the main effects of predation risk (tree versus lamp/sign-post), the main effects of food availability (food-bearing versus non-food bearing), and the main effects of season (autumn versus spring), and two-way interactions between these variables. These data conform to parametric assumptions (with homogeneity of variance-covariance matrices at a significance level above .001, equality of error variances above .05, as defined by Pallant, 2007), and due to the small sample size the more robust models have been reported.

Data were analysed using Microsoft Office Excel 2010 and SPSS 16.0 for Windows, with significant models reported to minimum 5% alpha level.

Results

The data demonstrated both floor and ceiling effects with a high proportion of cases where no caches were pilfered, a few cases where some of the caches were pilfered, and again a high occurrence of cases where all caches were pilfered (Figure 23). The number of cases where either no pilferage occurred or all caches were taken across the conditions is displayed in Table 11.

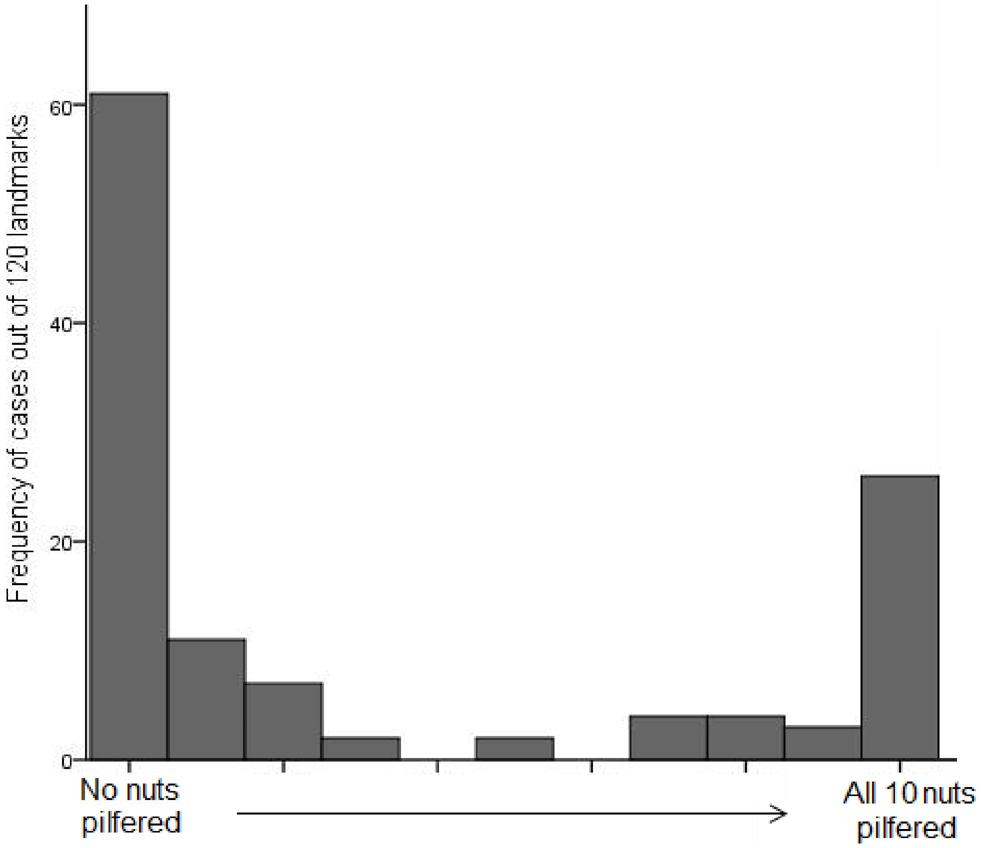


Figure 23. Histogram showing the frequency of combined pilferage at all landmarks.

Table 11. *Patterns of pilferage across the conditions (30 of each landmark type) and seasons (60 of each season) where 0% and 100% pilferage occurred. Total average pilferage rates were 42% (M = 4.23, SD = 4.25).*

	Number of cases	
	Zero pilferage	**Total pilferage**
Food-bearing tree	14	10
Non-food-bearing tree	16	5
Food-provisioned lamp/sign-post	15	6
Non-food-provisioned lamp/sign-post	16	5
Autumn	22	17
Spring	39	9

Total number of caches pilfered

Owing to the data having both floor and ceiling effects, analyses were conducted in terms of whether there was no pilferage, some pilferage, or total pilferage from the landmarks. A GEE was carried out and it revealed no main effect of predation risk (p = .102), no main effect of food availability (p = .306), no predation risk x food availability interaction (p = .597), and no food availability by season interaction (p = .595). However, there was a significant main effect of season, X^2 ($df = 1$, $N = 60$, $n = 120$) = 2.70, $p = .009$, with more total pilferage occurring in the autumn compared to the spring, displayed in Figure 24(a). There was also a significant predation risk x season interaction, X^2 ($df = 1$, $N = 30$, $n = 120$) = 8.03, $p = .005$, and follow-up contrast tests revealed that trees experienced the most total pilferage in the autumn and the least total pilferage in the spring in comparison to lamp/sign-posts, displayed in Figure 24(b).

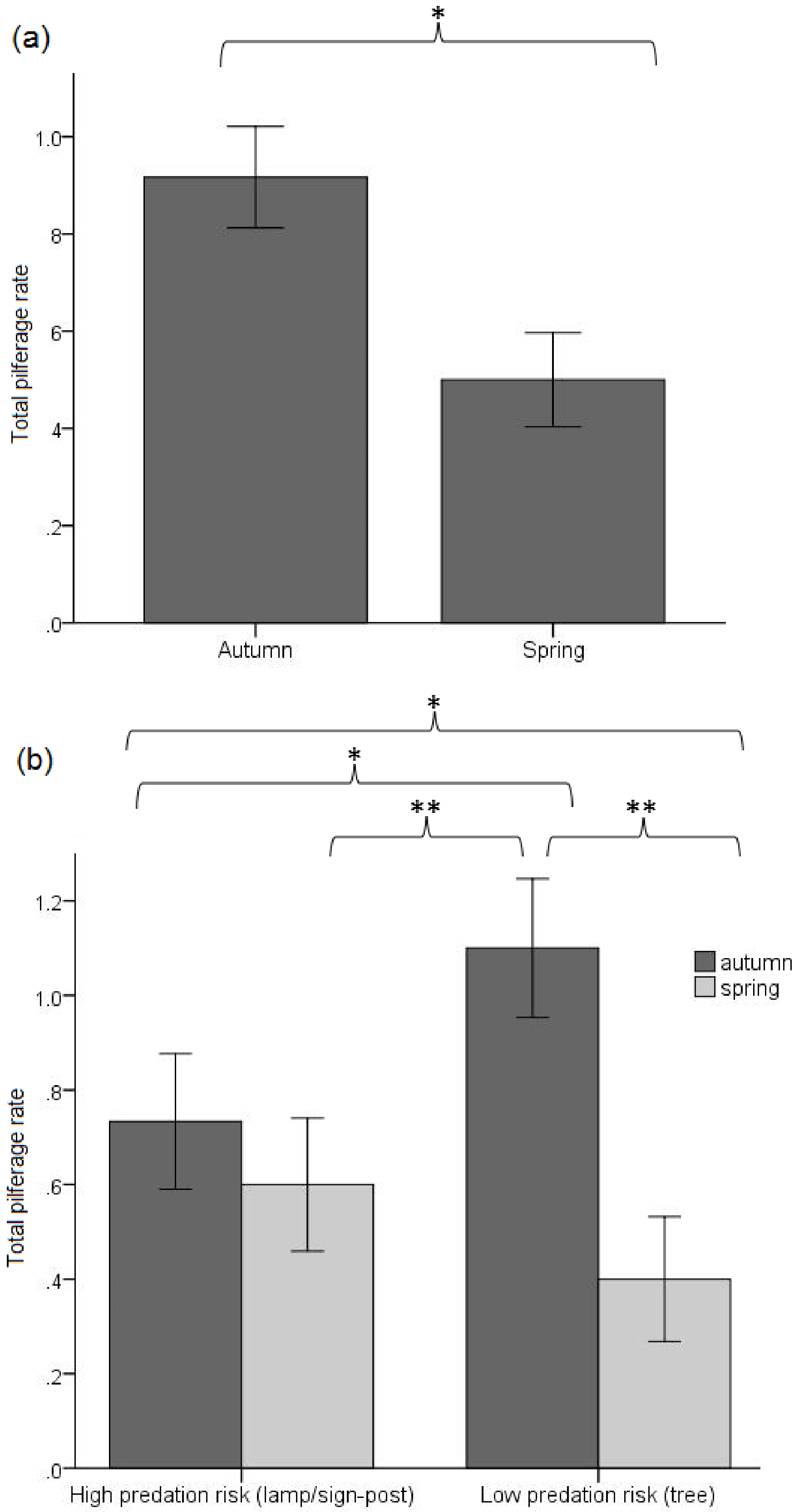


Figure 24. Rates of total pilferage across (a) seasons, and (b) trees and lamp-sign-posts across seasons. Bars represent ± 1 standard error. Note that “spring lamp/sign-posts” x “spring trees” approached significant at *p* = .070.

Caches pilfered over time

We compared whether there were differences in proportion of caches pilfered on the first three days after burying compared to the last three days. A paired samples t-test revealed a significant difference between the two measures, *t* (119) = 5.07, *p* = .001 (Partial Eta squared .18), with more caches being taken during the first three days of the experiment, which is displayed in Figure 25.

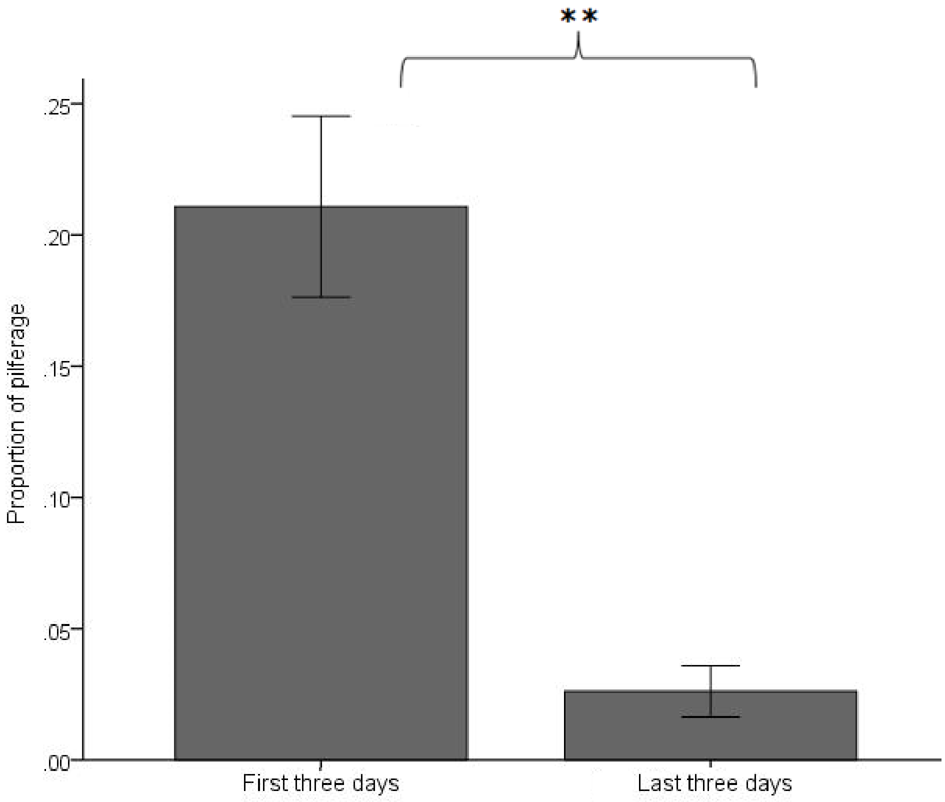


Figure 25. Graph showing the difference in proportion of caches pilfered between the first three days of pilferage with the last three days. Bars represent ± 1 standard error. ** *p* < .001.

Finally, we compared whether there were differences in mean pilferage at the first three days after burying with the last three days between the conditions. A three by two repeated measures ANOVA revealed that there was no main effect of predation risk (*p* = .487), no main effect of food availability (*p* = .071), no main effect of season (*p* = .361), no predation x food availability interaction (*p* = .441), and no season x predation interaction (*p* = .234), and no season x food availability interaction (*p* = .712).

Discussion

Overall, we found no effect of predation risk or food availability on total pilferage. However, there was an effect of season with more landmarks experiencing complete pilferage of their caches in the autumn than compared to the spring. There was also a mediating effect of predation risk upon season; in the autumn trees (low predation risk) were more likely to have all their caches removed from around them, and in the spring trees were least likely to have all their caches removed from around them, compared to lamp/sign-posts (high predation risk). We also found that more caches were pilfered during the first three days compared to the last three days of testing, but predation risk, food availability and season did not influence this outcome.

Previous research has indicated that caches buried close to trees are at higher risk of theft (Leaver et al. 2014; Stapanian & Smith 1978; 1986; Steele et al. 2014) which might be because naive competitors spend more time foraging in these locations for one of two reasons: because trees provided a reliable source of food from which to forage, and/or because trees provided an escape route from potential terrestrial predators, and cover from aerial predators. There is evidence to support both of these points of view; trees do provide optimal foraging locations because of their food availability (Brodin, 1993; Clark & Clark 1984; Janzen 1970; Tamura 1998; 1999; Tamura et al. 1999), as well as refuge and cover from predators (Stapanian & Smith 1978; 1986; Steele et al. 2014). However, it was not clear whether other possible landmarks that provided different combinations of these factors would also be subject to similar levels of pilferage. From the results of our study, we found that locations that differed in their food availability did not vary in their rates of cache pilferage. In terms of locations that differed in predation risk, we found that pilferage rates did vary but the relationship was complex: in the autumn pilferage was higher at trees, and in the spring pilferage was higher at man-made landmarks. We also incorporated the influence of season in our experiment and found that it influenced cache pilferage in the opposite direction to what we predicted, with higher rates of pilferage experienced during the autumn.

Overall pilferage rates

The data distribution for the total number of caches pilfered demonstrated floor and ceiling effects. There was a high occurrence of cases where no caches were pilfered, very few cases where only some of the caches were pilfered, and a relatively high number of cases where all caches were pilfered. In addition we also found that caches were more likely to be pilfered in the days immediately following when they were buried compared to the last three days. These results suggest two things: firstly, that squirrels visited our cache sites relatively soon after nuts were buried at them; and secondly, that once a pilferer had located one cache they would continue searching in the immediate area for more caches. This is in line with previous studies that report that more closely spaced caches are at greater risk of pilferage (e.g., Male & Smulders 2007b; 2008).

Research indicates that squirrels frequently re-locate their own caches (unpublished observations in Jacobs & Liman 1991; experimentally shown in Chapter 2), however it is unknown whether this is a strategy also used by pilferers within the same species to prevent a cacher from recovering their store. Throughout our study we monitored each landmark for evidence of eating around its vicinity, looking for discarded hazelnut pieces but none were ever found. In addition, on the one occasion when pilferage was filmed at a landmark, we recorded re-caching of all 10 nuts. Therefore, it is likely that when a cache was found that it was transported to be eaten or buried in another location, as opposed to close to where it was found.

Seasonal differences in pilferage rates

Food hoarding animals are reliant upon resources that are seasonally variable in predictable ways. Grey squirrels demonstrate seasonal differences in their foraging, hoarding and caching behaviour in response to food availability (Thompson 1978). In the current study we hypothesised that pilferage rates would be higher in the springtime when competition for recovering caches was high, in comparison to the autumn when competition for burying caches was high. However, we found the opposite with more incidents of total pilferage occurring in the autumn in comparison to the spring.

Our original prediction was based upon the knowledge that in the autumn squirrels spend more time caching mature husked nuts when they are plentiful in preparation for the coming months when there is less food to forage (e.g., Steele & Koprowski 2001; Hadj-Chikh et al. 1966). In the springtime when resources are scarce squirrels seek out and recover high energy food hoarded during the autumn to supplement their low energy (e.g., buds of trees) spring diet (Thompson & Thompson 1980). Therefore, it is possible that because squirrels generally spend more time foraging for nuts to cache in the autumn months that they were more likely to come across our artificial caches by chance, in comparison to the spring when they hoard less. In addition, when storing food a number of scatter hoarding species have been reported to return to their caches, recover and rebury them, which might help to reduce loss of stores to pilferers (reviewed and experimentally tested in squirrels in Chapter 2), as well as to refresh memory for their cache locations (unpublished observations of squirrels in Jacobs & Liman 1991). Consequently, engaging in this behaviour would also increase their encounter rate with our artificial caches in the autumn months. Alternatively, in the springtime squirrels recover their own caches but, because there are generally fewer caches to recover, they are less likely to engage in opportunistic pilferage.

Seasonal differences in aversion to predation risk

We also found seasonal differences in where squirrels pilfered in terms of predation risk: in the autumn, caches placed close to the refuge of trees experienced more pilferage compared to lamp/sign-posts, while in the spring there was a trend for man-made landmarks (that were more exposed to predators) to experience higher pilferage than trees. Some researchers have suggested that caches placed close to trees are at a higher risk of theft because trees provide a safer location to forage (Stapanian & Smith 1978; 1986; Steele et al. 2014). The data we collected in the autumn supports this point of view; however the data we collected in the spring is not consistent with this explanation.

There is a possible reason that we found a seasonal difference in pilferage at landmarks differing in predation risk, which integrates with the argument of Steele and colleagues (2014). Given that squirrels prefer to forage in safer locations, in the autumn when resources are plentiful they can be more selective about where they forage; choosing locations closer to trees which provide cover and an escape route from predators. However, in the spring when caches are depleting and other resources are limited, squirrels have to be less selective over where they forage in order to obtain sufficient resources; therefore, being less averse to predation risk helps them to meet this demand, and foraging close to other possible landmarks helps them increase the probability and speed that they will encounter a cache. This idea could be easily investigated by incorporating the study design of Leaver et al. (2014) into the current experiment: test different landmark types across different seasons, but also bury nuts at different distances to the landmarks in order to measure whether those buried closer to landmarks are pilfered at the same rates as those buried farther away.

Alternatively, the study design could account for the seasonal difference in pilferage at landmarks differing in predation risk. Specifically, because only the food bearing lamp/sign-posts were provisioned in the springtime, and the trees that would naturally bear food only in the autumn months were not provisioned, this could account for why there was a trend for pilferage rates to be higher at man-made landmarks, compared to the depleted food trees, in the springtime. In the current study trees that provided food in the autumn were not provisioned in the spring because it was expected that squirrels would have already learned these as locations that had a high food density. Whether they also learn to forage less in these locations in the springtime could easily be incorporated in a further study by consistently provisioning the food trees throughout seasonal changes in natural food availability. Nevertheless, it is evident that squirrels are pilfering from all types of landmark in both seasons, albeit less overall pilferage occurs in the springtime, and they can learn that man-made landmarks can be a source of food.

Using landmarks to pilfer

Overall, we found that all four types landmark were pilfered from, including the un-provisioned lamp/sign-posts which offered no obvious benefits to foragers. However, given that our current data found that pilferage from all types of landmark did not differ in terms of food availability or predation risk alone (only in relation to season), our results show that both natural and man-made landmarks are high risk locations to bury caches. Furthermore, because there was a trend for pilferage rates to be higher at lamp/sign-posts in the spring in comparison to trees, this indicates that squirrels might forage close to these type of landmark, and possibly that man-made landmarks might be used as cues during cache pilferage. In the laboratory grey squirrels have been trained to locate hidden food using landmarks and even show a preference for landmarks and visual cues when they were able to use olfaction (McQuade et al. 1986).

Throughout this study we refer primarily to the pilfering behaviour of squirrels, however we cannot be 100% certain that squirrels were always the pilferers of our caches, even though measures were taken to monitor this. Nevertheless, if non-squirrel species also pilfered, our data still reflect the cache locations that are at greater risk of theft from other species. Indeed squirrels compete with both conspecifics and heterospecifics that also store and pilfer food (reviewed in Chapter 6).

In a situation where the pilferer has not witnessed a cache being made, very little is known about how pilferers steal the stores of others across a range of scatter hoarding species. From the existing literature, we know that squirrels and other scatter hoarders can learn to associate visual cues with cache locations which can be used to assist recovery (e.g., grey squirrels: Macdonald 1997; McQuade et al. 1986); however, the majority of these studies are either tested under laboratory conditions or use cues that subjects would not naturally be exposed to in field conditions. Across the range of scatter hoarding species there is still very little known about how pilferers steal caches. Therefore, this study provides a platform for future research to investigate more about the behaviour of cache pilferers. For instance, it would be interesting to investigate in the field if there is an optimal distance at which caches are placed from landmarks, so that the landmark still acts as a cue for the caching individual, but the cache is placed far enough away to limit pilferage from thieves using visual cues to pilfer. Such a study would require monitoring natural caches and individual squirrels over a long period of time in order to provide data about cache recovery, which is lacking in the grey squirrel literature.

Cachers versus pilferers

A final matter that needs revisiting is the behaviour of the caching individual. If certain locations provide easier and more accurate retrieval for a cacher, and pilferers evolve to more frequently visit these locations, then these locations would no longer provide benefits to the caching individual.

Some authors suggest that pilferage may be tolerated among solitary hoarders if a large enough number of pilferers also cache food, thus allowing pilfering to be reciprocal. We know from the literature that grey squirrels actively engage in a variety of behaviours to minimise the loss of their caches to pilferers (reviewed in Chapter 2), suggesting they do not willingly share their food hoards (Leaver et al. 2007). However, given the number of caches pilfered in the current study, they also appear to be well adapted as cache pilferers. Moreover, Vander Wall and Jenkins (2003) suggest that grey squirrels are likely to be tolerant of reciprocal cache pilferage, despite not being altruistic cachers. Thompson and Thompson (1980) estimate that wild squirrels recover around 84% of caches. Therefore, it seems appropriate that cachers should either avoid caching in locations where high pilferage occurs, or engage in behaviour that serves to offset the increased risk of pilferage. While at the same time, pilferers adapt ways to enhance their opportunity for cache theft: VanderWall and Jenkins (2003) suggest that if a species ‘cannot avoid or prevent pilferage’ (p. 661) then they might respond by investing their energy into being an efficient pilferer.

One study has highlighted how caching and pilfering strategies can exist within the same system among grey squirrels. As well as finding that rates of theft of artificial caches was lower beyond the canopy of trees, Steele et al. (2014)

found that grey squirrels preferentially cached more profitable food items in areas that were more exposed to predators, beyond the canopy cover of trees, compared to less profitable items that were cached in locations associated with high pilferage. They suggest that squirrels trade-off decisions about predation, food value and pilferage, which can affect caching strategy. Stapanian and Smith (1986) report similar behaviour in fox squirrels who prefer to cache in more exposed locations, as opposed to close to cover. They suggest that cache-owners can move quickly and deliberately between their remembered caches in exposed areas, but thieves must forage much more slowly in order to pilfer caches using olfactory cues. Furthermore, Devenport, Luna and Devenport (2000) investigated cache placement tactics in thirteen-lined ground squirrels, *Spermophilus tridecemlineatus*, who are reported to both larder and scatter hoard, and found that squirrels avoided placing caches close to ‘prominent objects’ which might help to reduce the chance of discovery by competitors.

Further field studies are required to understand the behaviour of pilfering scatter hoarders in order to determine how it fits in with the strategies that cachers engage in to avoid pilferage. However, observing cache recovery behaviour is difficult in the field. Individual caches need to be marked and monitored for extended periods of time, and when a cache is uncovered you need to know whether the individual is recovering its own cache or pilfering. While this is much easier to achieve with captive studies, they do not provide enough space for cache placements to be interpreted on an ecologically relevant scale. Thus future research of this kind should continue to study behaviour in the field, perhaps using camera traps or closed-circuit television cameras, which might help to overcome some of the problems associated with studying wild squirrels.

Conclusion

Bugnyar & Kotrschal (2002) suggest that cachers and pilferers are engaged in an ‘evolutionary arms race’, where cachers develop methods to minimise the risk of cache pilferage, while pilferers develop strategies that allow them to more easily locate and steal others caches. This relationship has received little examination among scatter hoarding Paridae and Rodentia and, therefore, the current study investigated by what means pilferers might increase their success at stealing caches. Combined with the findings from previous studies that show that pilferage rates are higher closer to trees, the results of the current study suggest that landmark use, predation risk and seasonality might play a role in pilferage behaviour. However, the mechanisms by which pilferers locate caches are still far from understood.

Chapter 6: Behavioural responses of wild Eastern grey squirrels to auditory playbacks of competitors and predators.

Introduction

Grey squirrels frequently forage within a social context of conspecifics, heterospecific competitors and potential predators.. Social foraging can benefit the individual in a number of ways, including providing information about optimal foraging conditions and reducing costs associated with predation risk. However there are fitness costs associated with increased competition from social foraging, and there is some evidence to suggest that there might be a trade-off between reducing the risks posed by predation and competition. In the current study we examined whether grey squirrels are differentially sensitive to different cues of risk while foraging, and we looked at how their behaviour is modified in response to social and predatory risks.

Foraging among conspecifics: the costs and benefits

The social environment can influence an individual’s decisions on where and when to forage. Foraging alongside others can benefit individuals by allowing them to more easily locate resources through a process of local enhancement (Adams & Jacobs 2007; Heyes et al 2000; Galef & Giraldeau 2001), and informing them about the optimal place to search for food (Galef & Giraldeau 2001). Conspecifics can provide information about when it is safe to forage (Galef & Giraldeau 2001), reduce the need for vigilance during feeding (Lima 1995), and reduce predation risk by dilution (Bednekoff & Lima 1998; Elgar 1989; Galef & Giraldeau 2001; Rausch et al. 2012).

However, social foraging also presents a fitness cost to the forager. Individuals must compete with one another for the same food resources while foraging and during cache recovery, and increased competition can increase the possibility of antagonistic encounters (Gerber et al. 2004). Dominant grey squirrels have been found to use their rank to monopolise a food patch, to sequestering food to eat and store (reviewed in Chapter 4). Some grey squirrels will act in ways that help to avoid antagonistic interaction with conspecifics while foraging, such as transporting food away from a food patch (Hopewell et al 2008), increasing their vigilance levels (Tarigan 1994), or demonstrating alarm behaviour including tail flagging, barking and vigilance which may serve to ward off potential competitors (Partan et al. 2010; Partan et al. 2009). All these behaviours can only be performed at a costs to time spent foraging.

In addition, because grey squirrels are a scatter caching species, they must also compete for cacheable items to recover and consume at a later time when there is less food available. They have been found to engage in different behavioural strategies to offset the risks of caching while conspecifics are present. Grey squirrels modify their caching behaviour in the presence of conspecifics in ways which reduce the possibility that their food stores might be stolen (Hopewell & Leaver 2008; Hopewell et al. 2008; Leaver et al. 2007), and they have been reported to make empty caches in the presence of conspecifics, may serve to confuse potential theives (Steele et al. 2008).

Foraging among competing heterospecifics: the costs and benefits

Foraging in the presence of heterospecifics that share similar food sources, habitats or predators may have some of the same advantages as foraging with conspecifics. Avarguès-Weber, Dawson & Chittka (2013) suggest that heterospecifics could provide as much valuable information as conspecifics. For instance, some sciurids eavesdrop on the alarm calls of sympatric bird species in order to obtain information on predation risk (red squirrel: Randler 2006a; Eastern chipmunk: Schmidt, Lee, Ostfeld & Sievingc 2008). However, very few studies have investigated whether heterospecifics could enhance information about optimal foraging locations, with the majority of these on invertebrates (Avarguès-Weber et al. 2013), though squirrels are known to forage at the same food patches as other species and compete with them for access (Bekoff et al. 1999; Fisler 1977; Wauters et al. 2000; 2001).

As with conspecifics, there are disadvantages as well as advantages in foraging with heterospecifics. Corvids live alongside grey squirrels and compete for the some of the same resources while foraging and storing food. Some species of corvid could pose a particular threat because they have been demonstrated to possess good observational spatial memory, which can increase their accuracy for locating caches they have seen being made by others (reviewed in Chapter 3). There is also evidence of corvids following grey squirrels and raiding their caches after observing them being made (Vernelli 2013). Two studies have directly investigated the role that corvids might play as competitors for caches. Schmidt and Ostfeld (2008) used playbacks of jay vocalisations at varying distances to simulate pilferage risk to caching grey squirrels. They found that squirrels reduced their effort when recovering cached food if recordings of blue jays were played closer to the foraging patch while they were caching. However, when actually storing food, squirrels do not appear to be sensitive to a corvid audience in the same way as they are to a conspecific audience. Leaver et al. (2007) reported that grey squirrels spaced their caches father apart in the presence of conspecifics, and oriented with their backs to conspecifics when caching, but they did not do this when caching in the presence of corvids. They suggest that facing away from corvids while caching may not provide the cache protection advantages that it has to a conspecific audience, given that corvids can fly to observe the caching squirrel from an aerial location. Given that corvids pose similar risks as conspecifics to foraging and caching grey squirrels there are good reasons to expect them squirrels to react to them as heterospecific pilferers.

Predation risk while foraging

A further factor that impacts upon foraging is the threat of predation. Urban grey squirrels are prey to a variety of species including red foxes (Booth et al. 2012; Müller-Schwarze 2009; Rausch et al. 2012), raptors (Temple 1987) and domestic animals (Makowska & Kramer 2007). Frequently there is a trade-off between foraging efficiency and reducing predation risk. Grey squirrels engage in anti-predator behaviourincluding bipedal vigilance (Makowska & Kramer 2007), and alarm vocalisations (Bakken 1959; Horwich 1972; Lishak 1977; Partan et al. 2010; Partan et al. 2009), all of which can incur a cost to time spent foraging (Makowska & Kramer 2007; Shonfield 2011). Predation risk also affects decisions about where to forage and for how long. In locations where predation risk is high grey squirrels reduce their foraging time compared to areas under tree canopy or shade (Booth, et al. 2012; Bowers et al. 1993; Brown et al. 1992; Kilpatrick 2003; Newman et al. 1988), and will transport food to eat in an area of cover (Lima & Valone 1986; Lima et al. 1985).

However, often locations that are less exposed to predation also have increased foraging competition. Thus, sometimes individuals forage and cache in locations more exposed to predators in order to avoid interactions with more dominant competitors (crested tit, *Parus cristatus*: Lens, Adriaensen & Dhondt,1994; willow tit: Ekman 1987; Koivula et al., 1994; Lahti et al. 1998). Grey squirrels have also been found to trade-off the risk of cache theft against the risk of predation, preferring to cache more profitable food items in open areas exposed to predators compared to storing non-profitable items closer to tree-cover where there is also a higher risk of cache theft (Steele et al. 2014). These studies demonstrate that foraging individuals do not always act in ways to simply minimise predation risk, but that the role of the social environment heavily influences foraging and hoarding decisions about predation risk. However, less is known about what contribution social and predatory risks make to overall foraging decisions.

Risks while foraging: conspecific-and heterospecific-competition and predation risk

It is clear that squirrels face a multi-way trade-off in choosing where and when to forage, in terms of the costs and benefits of social foraging and the costs of predation. They engage in different behavioural strategies to offset these risks while foraging and storing food, such as engaging in vigilance behaviour, changing how they forage, cache or recover food. While elements of this trade-off have been considered before so that we know how grey squirrels respond to multiple cues, the full system has not. The current study isolates responses to these different risk factors to determine what contribution they make to foraging decisions.

In the current study we used auditory playbacks to simulate some of the risks that wild grey squirrels might face while foraging: risks posed by other squirrels, risks posed by other species that compete for the same resources as squirrels (corvids), and risks posed by predators. We monitored behavioural changes in alert behaviour (vigilance, escape and vocalisations) and foraging duration and distance from safety, across three time periods (before, during or after playback). Auditory playbacks provide a powerful tool in many behavioural studies of wild animals and can be particularly useful for monitoring behavioural responses to risk cues (e.g., Murphy, Lea & Zuberbühler 2013). This technique allowed us to isolate responses to the three different risk factors in order to determine their relative significance in modifying squirrels' foraging and alert behaviours.

We predicted that if squirrels respond to the calls of conspecifics and heterospecifics as potential competitors for resources then they should act in ways which maximise foraging, including engaging less time in alert behaviour (being vigilant, escaping to areas of safety, vocalising) and more time spent foraging. On the other hand, if they respond to conspecifics and heterospecifics as sources of antagonistic interaction then we predicted that they would act in ways to minimise potential contact by increasing their alert behaviour, and foraging farther away from trees. Finally we predicted that the predator playback would increase the time squirrels engaged in alert behaviour, which would be performed at a cost to foraging, and that they would respond by seeking areas closer to safety, or escape into trees.

Method

Study sites and sample

Observations were carried out in urban parkland of towns in South and East Devon between 0900-1600 hours from October 2012 through January 2013, to coincide with the peak natural caching patterns of grey squirrels in this region. Sites were selected where squirrels were foraging or had previously been seen foraging. We visited a total of 97 different locations, observing one squirrel at each site. Forty of these locations provided satisfactory independent experimental observations of adult squirrels that remained in view for the necessary length of time to conduct observations (criteria are discussed later in detail). Sites were more than 300 metres apart from one another (monitored using Free GPS iPhone application by Code Burners and verified by www.itouchmap.com) to avoid overlapping home ranges between individuals (the maximum known linear measure of home range size recorded for a grey squirrel is 136.7 metres: Doebel & Mc Ginnes 1974, a measure which has been used for the same purpose in other recent grey squirrel studies, e.g., Getschow et al. 2013); therefore we can say with a good degree of certainty that our observations at different sites are independent (*N* = 40).

Experimental design and playback stimuli

This study used a between subjects design so that each of the 40 squirrels was exposed to one of four playback conditions: squirrel calls (N=10), corvid calls (N=10), predator calls (N=10), or white noise (N=10). Each playback was unique and only used once during the study, to minimise the possibility for pseudoreplication and control for the potential referential content of the calls (Kroodsma 1989), excluding the white noise playback which was used as a control stimulus and played at ten different sites, see Table 12. The order that each playback stimulus was presented was predetermined so that there was a equal number of stimuli for each of the four conditions.

Table 12. *Descriptions of playbacks used as stimuli. All calls were obtained from the National Sounds Archive, London, UK, FreeSound.org and personal recordings. Each stimulus was played only once, excluding white noise.*

Condition	**Stimuli**	**Description and context**
Conspecific	10 x different combination “kuk” and “quaa” calls (Horwich 1972; Lishak 1984).	These are thought to be alarm vocalisations produced by grey squirrels; they are produced separately as well as in combination with one another, and comprise a similar frequency composition and sound intensity.
Heterospecific competitor	2 x different raven calls, “gurgling croak” (http://www.allaboutbirds.org/guide/common_raven/sounds);	These are ‘contact calls’ made by adult corvids, thought to be used to communicate to other birds at a distance (Westerfield, 2011), and

	4 x different crow*, Corvus corone*, calls, “multiple caw” (Westerfield 2011); 2 x different magpie calls, “chacker chacker” (Redondo 1991; http://www.garden-birds.co.uk/birds/magpie.htm); 2 x different rook calls, “multiple caw” (Røskaft & Espmark 1982).	all have a similar amplitude range. Species were selected that known to compete for resources with squirrels and reside in similar habitats. Calls were selected to be similar in structure to one another.
Predator	1 x buzzard, Buteo buteo, circling call (Krüger 2002); 2 x different goshawk, *Accipiter gentilis*, calls, “agitated wail” (http://www.allaboutbirds.org/guide/northern_goshawk/sounds); 1 x red tail hawk, *Buteo jamaicensis*, “kee-eeeee-arr” flight scream (http://www.allaboutbirds.org/guide/red-tailed_hawk/sounds); 1 x kestrel, *Falco tinnunculus*, “klee-klee-klee” excitement call (http://www.allaboutbirds.org/guide/american_kestrel/sounds); 2 x different peregrine, *Falco peregrinus*, “kak, kak, kak” pair calls (http://www.allaboutbirds.org/guide/Peregrine_Falcon/sounds); 3 x different red fox, *Vulpes vulpes*, adult yell barks (Newton Fisher, Harris, White & Jones 1993); 2 x different Labrador dog, *Canis familiaris*, play barks (Yin & McCowan 2004).	These predators are common to urban-living squirrels, and all stimuli originate from adult individuals. The raptor calls are those that are normally produced in a flight context (thus, not produced by hunting birds), and the canid vocalisations are those produced in a play context. Thus, the playbacks are purely to simulate the presence rather than immediate threat. Calls were selected to be similar in structure to one another.

Control	1 x white noise recording used ten times, generated by Audacity 2.0.3.	Previously demonstrated to be a successful control condition with squirrels (Schmidt & Ostfeld 2008).

Each audio stimulus was taken from digital recordings of vocalisations coming from a single individual. Using Audacity 2.0.3, recordings were edited to be monophonic, background noise was removed, and they were cut to provide 15 seconds of playback. During the 15 second playback the audio was intermittent rather than continuous, but it was edited so that there was no more than 3 seconds of silence between each sound made. During the 15 seconds of playback each of the sounds emitted was unique, in that they were not digitally edited to be repeated, but naturally followed on from one another in the original digital recording. All of the types of vocalisations chosen ranged between 50-100dB and were relatively similar in structure to one another across categories (Figure 26).

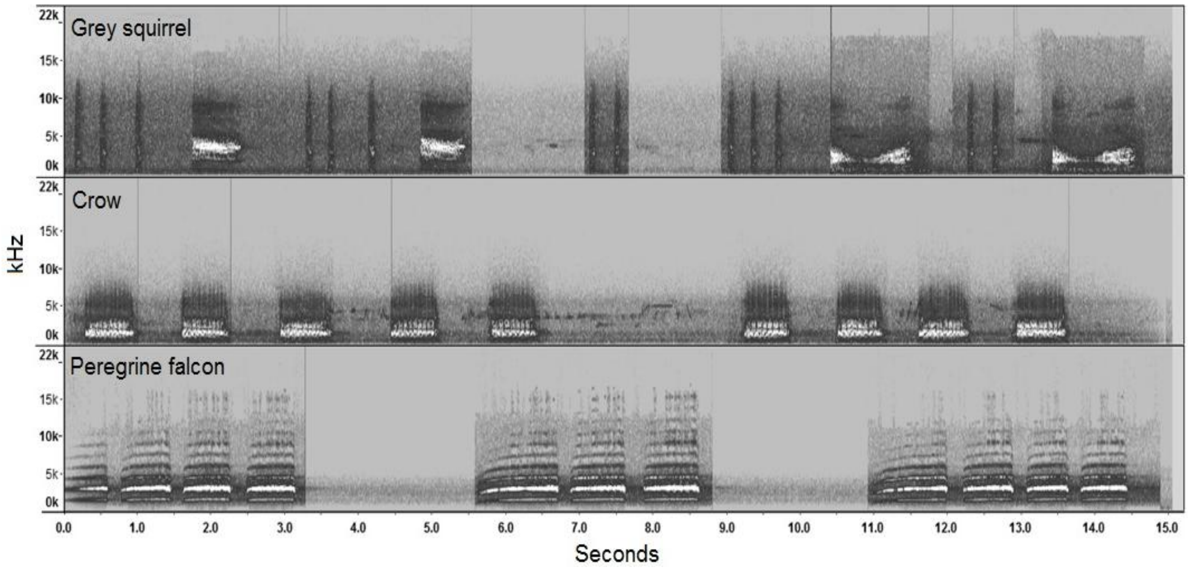


Figure 26. Spectrogram of typical playback for each of the experimental conditions (generated using Audacity 2.0.3).

The calls were levelled using iTunes and the amplitude for each call was adjusted using a sound level meter (Cirrus Research Limited Sound Level Meter, verified using Free GPS Version 3.6.2 iPhone application) at 1 metre from the source in the type of natural environment in which the experiments took place, to the average natural peak amplitude of the stimulus species:

average squirrel playback amplitude was at a natural peak of 70dB (Lishak 1984, 1982), average corvid peak playback amplitude was 75dB (Blumstein, Daniel, Griffin & Evans 2000; Goodson & Adkins-Regan 1997; Heinrich 1988; Searcy & Caine 2003), average predator calls peaked at 80dB (raptor: Chu, 2001; Jurisevic & Sanderson 1998; Krüger 2002; Searcy & Caine 2003; fox: Frommolta, Goltsman & Macdonald 2003; domestic dog: Randler 2006b); and white noise was at a constant 90dB (which has been used as the maximum sound intensity in previous playback studies with grey squirrels, e.g., Schmidt & Ostfeld 2008). Calls were played using an iPhone4S (volume adjusted to pre-determined dB level for each call) connected by a 25 metre audio cable to an X-mini™ II speaker at full volume, so that the observer could operate the calls at a distance to the speaker away from the main observation area. Pre-determined criteria established when calls would be played according to several factors, including the distance of the focal individuals (discussed later in detail).

Procedure and measures

Three principal observers were involved in collecting data for this study. We achieved high levels of inter- observer reliability (between 76-100% agreement for all measures, calculated using the index of concordance technique reported in Martin & Bateson 1993), but worked in pairs for the majority of observations (N = 27 out of 40) to ensure consistency in recording. Observers sat at the edge of the observation site (starting observations at a minimum of approximately 20m from the nearest squirrel), close to shrubs or a tree so they appeared less exposed. The speaker was placed on the ground in the centre of the observation area, a minimum of 5m away from the base of a tree/shrub, covered with leaves or grass, and operated from a distance using an iPhone4S. Observation of a focal individual would commence five minutes after arriving at the study site to allow the animal time to habituate to our presence and to minimise potential disturbances in the data.

A focal squirrel was selected using opportunity sampling of any squirrel that was on the ground, and behavioural data were recorded using a digital audio voice recorder (iPhone4S or Olympus DM-450). Continuous sampling was used to monitor the start and end times of all behaviours and changes in location of the focal squirrel. Observers recorded the following behaviours, focussing on activities that might affect fitness (McGregor 2000). (1) Vigilance: while on ground, individual stops current behaviour, becomes bipedal with body in a stretched upright position with head high, ears forward, and not eating or manipulating food, but can be holding food, may also be tail flagging, or foot tapping (adapted from Blumstein & Arnold 1995, & Partan et al 2010). (2) Escape: fleeing to an area of refuge. (3) Foraging: searching for food, manipulating items, eating food, carrying food, caching food; can be bipedal or quadrupedal, but must be on the ground. (4) Vocalisation. (5) Average distance the squirrel was to an area of refuge to the nearest .5m: refuge included any natural or man-man structure that would provide safety from a terrestrial or aerial predator. We also made a deliberate effort to monitor any deceptive caching behaviour that occurred as defined by Steele et al. (p. 706, 2008); this behaviour has not been documented among populations of grey squirrel outside the two in their study.

Before commencing playback, observers collected 3 minutes of continuous behavioural data from one focal squirrel. After this time the 15 second auditory stimulus was played if the conditions adhered to the following criteria: the squirrel had remained on the ground for a minimum of 75 seconds immediately prior to the onset of the playback, had not engaged in alert behaviours (vigilance, vocalisation, escape) during the prior 30 seconds, was within 10-30 metre range of the speaker, and had not been exposed to the natural auditory presence of conspecifics, heterospecific competitors, or predators. Observers continued watching the focal squirrel for a further 3 minutes after the playback had ended if it remained in sight. If it escaped up a tree and was still visible we continued to monitor behaviour for a further 3 minutes, and waited to record its latency to return from the tree if this continued beyond 3 minutes (maximum latency was 196seconds). A total of 56 out of 97 observations were discarded before playback commenced because the observations did not meet these criteria (essentially squirrels were not in sight long enough), and one observation was discarded during playback because the focal squirrel went out of sight at the time of the playback and so we could no longer be certain of its identity when it returned into view.

Statistics

We carried out a 3 x 4 mixed design repeated measures ANOVA to examine the main effects of time-period (pre-, during- and post-playback) and condition (conspecific, corvid, predator, control), and the time-period by condition interactions on the following dependent measures: vigilance duration, foraging duration and foraging/vigilance distance to refuge. Data for the measure 'distance' were transformed using a square root transformation which corrected violated assumptions of sphericity, homogeneity of variance and equality of covariances. We used the more robust Pillai's Trace significance test where $P \leq 0.05$ was the criterion to further examine the outcome of the model. All follow-up pairwise comparison contrast tests were conducted with a Bonferroni adjustment to account for multiple comparisons.

We performed a chi-square analysis to assess differences between conditions and time-periods on frequency of escape behaviour.

Finally if the focal squirrel had responded to the playback by demonstrating any alert behaviour (the individual stopped foraging, and commenced vigilance, vocalisation, or escape behaviour during the stimulus playback) we measured the duration it took for the squirrel to resume foraging from the time the call was played. Data were transformed using a square root transformation which corrected violated assumptions of homogeneity of variances. A one-way between subjects ANOVA was conducted to examine differences in latencies between the four conditions, and subsequent planned follow-up pairwise comparison contrast tests were conducted using a Bonferroni adjusted alpha level.

We used Microsoft Excel 2010 and SPSS Version 16.0 to carry out the analyses.

Results

Descriptive statistics for vigilance and foraging durations and distance to refuge across the 4 playback conditions and during the three time periods are displayed in Table 13.

Table 13. *Descriptive statistics showing mean (and standard deviation) of behaviour during the three playback periods.*

	Conspecific ***n*=10**			**Corvid** ***n*=10**			**Predator** ***n*=10**			**Control** ***n*=10**		
	Pre	During	Post	Pre	During	Post	Pre	During	Post	Pre	During	Post
Vigilance duration /seconds	1.54 (.73)	6.00 (2.04)	4.14 (1.55)	2.96 (1.50)	5.40 (2.25)	2.10 (1.28)	.60 (.35)	11.10 (1.84)	3.66 (1.46)	2.12 (.76)	2.10 (1.14)	.70 (.41)
Foraging duration /seconds	9.60 (1.73)	8.70 (2.13)	7.36 (1.75)	11.26 (1.41)	8.10 (2.35)	10.70 (1.77)	12.40 (1.25)	1.80 (1.16)	7.80 (1.84)	10.92 (1.39)	11.40 (1.69)	9.74 (1.39)
Distance to refuge /metres	2.19 (.72)	2.07 (.56)	1.34 (.46)	.89 (.24)	1.65 (.51)	1.46 (.37)	4.84 (1.54)	2.75 (.96)	1.54 (.49)	3.48 (1.09)	5.64 (2.40)	4.50 (2.04)

Durations and distances of foraging and vigilance

A mixed ANOVA (with condition as between-subjects factor and time-period as within subjects factor) showed no main effect of condition on distance to refuge ($p > .05$), vigilance duration ($p > .05$) or foraging duration ($p > .05$) and no main effect of time-period on distance to refuge (lower bound test, $p > .05$). There were significant main effects of time-period on vigilance duration ($F_{2,72} = 14.11$, $p < .001$, sphericity assumed) and foraging duration ($F_{2,72} = 6.40$, $p = 0.003$, sphericity assumed), both with a moderate effect size (Partial Eta squared .28 and .15 respectively). There was no time-period by condition interaction on distance to refuge (lower bound test, $p > .05$), but there was a significant time-period by condition interaction on vigilance duration ($F_{6,72} = 3.67$, $p = 0.003$, sphericity assumed) and foraging duration ($F_{6,72} = 3.40$, $p = .005$, sphericity assumed), both with a moderate effect size (Partial Eta squared .23 and .22 respectively).

Subsequent planned contrast tests were carried out using a Bonferroni adjusted alpha level ($p \leq .016$) for the main effects of time period on vigilance and foraging durations, their results of which are included in Figure 27. For vigilance duration there were significant differences between the pre- and during-playback conditions ($p < .001$) and between the during- and post-playback conditions ($p < .001$). Figure 27(a) shows that squirrels spent significantly more time being vigilant when the call was being played compared to the pre- and post-playback time periods, indicating that they attended to the playbacks. For foraging duration there was a significant difference between the pre- and during-playback conditions ($p = .002$), and the differences between the pre- and post-playback conditions approached significance ($p = .028$). Figure 27(b) shows that squirrels spent significantly more time foraging prior to the playback compared to when the call was being played, and there was a trend for them to spend more time foraging after the call had been played compared to when the call was being played.

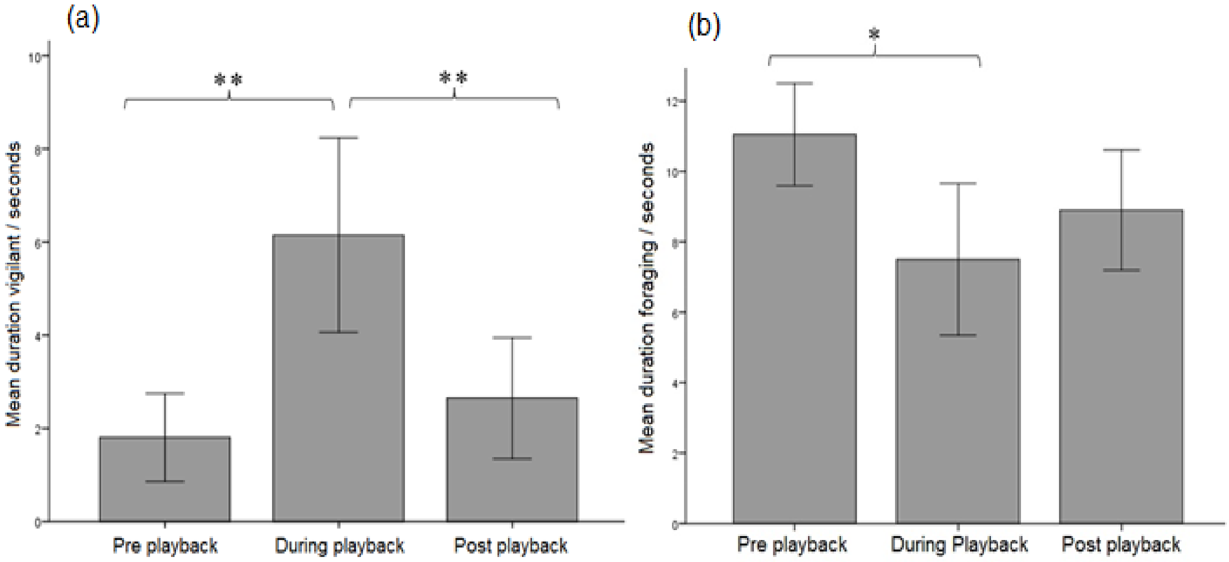


Figure 27. The effects of time-period on (a) vigilance and (b) foraging behaviours, including outcome of planned follow-up analyses. * $p < .05$, ** $p < .001$, and error bars represent 95% confidence intervals.

For the time-period by condition interaction we conducted planned follow-up analyses to examine differences between the four conditions at the 'during-playback' and post-playback periods. We conducted a ANOVA with condition as a fixed factor and vigilance duration during playback and foraging duration during playback as dependent measures. During playback we found significant effects of condition for vigilance duration ($F_{3,36}$ = 3.98, p = .015) and foraging duration ($F_{3,36}$ = 4.64, p = .008), both with a moderate effect size (Partial Eta squared .25 and .28 respectively), but there were no significant differences between conditions post-playback (p > 0.05). Subsequent planned contrast tests using a Bonferroni adjusted alpha level ($p \leq .01$) revealed significant differences between both vigilance duration and foraging duration for the predator and control conditions during playback (p = .002, p = .001 respectively), illustrated in Figure 28. During the experimental playback period, squirrels exposed to predator calls spent significantly more time being vigilant compared to the control condition, and spend significantly less time foraging than during the control condition.

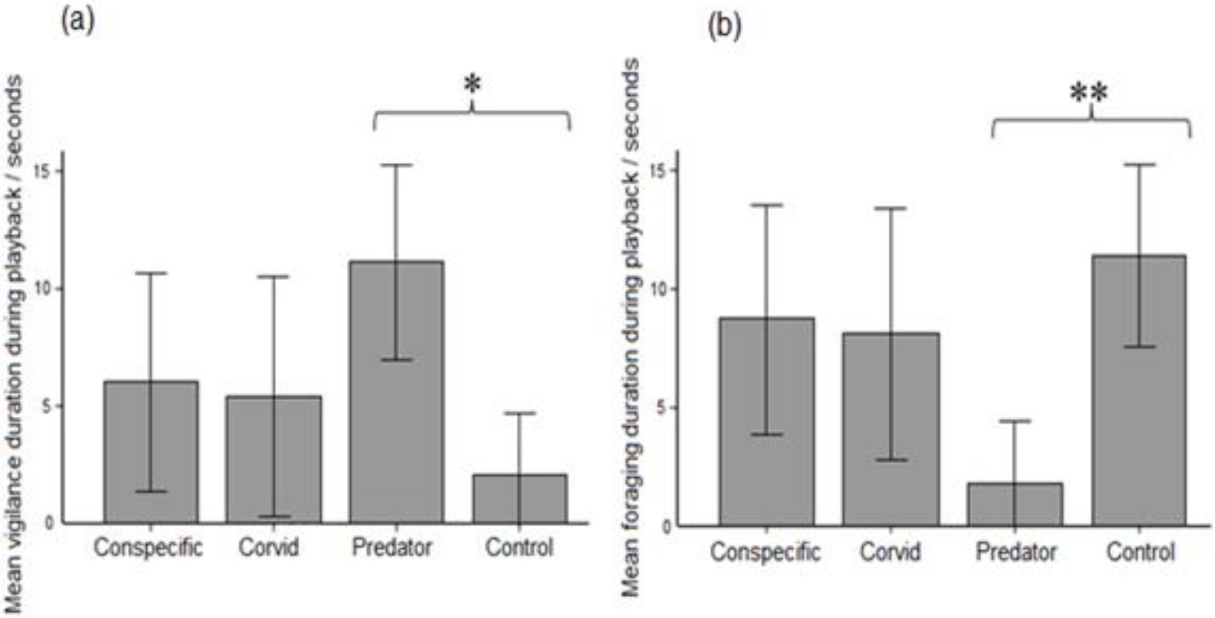


Figure 28. The effects of condition on (a) vigilance duration and (b) foraging duration. The outcome of the planned follow-up analyses conducted on the time-period by condition interaction are displayed. * $p < .05$, ** $p < .001$, and error bars represent 95% confidence intervals.

Frequency of escape behaviour

A chi square test was carried out to assess differences between conditions and between the time periods for frequency of escape behaviour. We did not find any significant differences in the amount of escape behaviour demonstrated between the conditions or for the different time periods ($p > .05$).

Latency to resume foraging post-playback-initiated-alert-behaviour

During all playbacks, the behaviour of focal squirrels was observed and defined as follows: no response, whereby the focal squirrel did not change from foraging to any alert behaviour during playback, and appeared to ignore the stimulus (conspecific condition $N = 1$, corvid $N = 1$, predator $N = 0$, control $N = 7$), or alert behaviour (as previously defined). Figure 29 shows latency to resume foraging after displaying alert behaviour during playback, which reveals that squirrels responded similarly to the conspecific and corvid playbacks, and both latencies to return to foraging were longer than the control condition. They took even more time to resume foraging behaviour when exposed to the predator playback compared to the three other conditions. These data were analysed using a one-way between subjects ANOVA which revealed a statistically significant difference between the conditions ($F_{3,36} = 26.90$, $p < .001$) with a large effect size (Partial Eta squared .69). Subsequent planned contrast tests using a Bonferroni adjusted alpha level ($p = .008$), revealed significant differences between all conditions ($p < .001$), excluding the conspecific and corvid conditions whose condition means were not significantly different from one another ($p > 0.008$), see Figure 29.

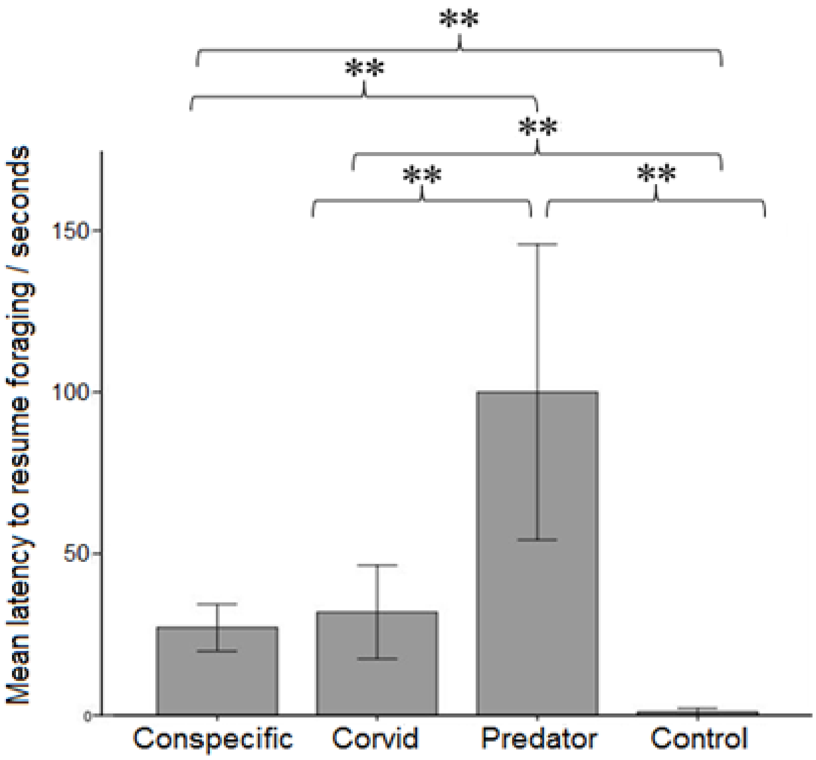


Figure 29. Differences in mean latencies to resume foraging across the different playback conditions if alert behaviour was demonstrated. ** *p* > .001, and error bars represent 95% confidence intervals.

Incident of 'deceptive' caching

Of the 97 locations visited while collecting behavioural observations we witnessed one occurrence of a 'deceptive caching' event that adhered to the description of Steele et al. (2008). A systematic description of the observation is presented in Table 14. We started observing the focal squirrel when it was approximately 15m from 5-10 other squirrels, however, it then moved to an area that was more than 20m away from any competitor species, which is when the conspecific stimulus was played. The 'deceptive cache' was observed 49 seconds after the playback had ended while the squirrel was still in the same approximate location. Throughout observations the experimenter remained approximately 25m away from the focal squirrel, monitoring behaviour using binoculars and a digital voice recorder, and joined by another person that was an untrained observer. The observation took place at Higher Cemetery, St Mark's Avenue, Exeter on 11th December 2012.

Table 14. *Systematic observation of a possible 'deceptive caching' event. The focal squirrel was exposed to the playback at 16minutes 3seconds into observation, and the 'deceptive caching' occurred at 17minutes 7seconds.*

Behaviour description	**Time**
At the time of the playback, the focal squirrel responded by escaping in opposite direction to the call, while nut carrying, and jumping onto a gravestone, where it then sat being vigilant.	16m 03s
While on the gravestone, it manipulated a nut with its paws and mouth, and while intermittently eating the nut.	16m 32s
It then jumped off grave, while nut carrying, and made several digs at the base of the grave.	16m 37s
Moving 1m away from the grave it had previously sat on, it dug a hole while nut carrying.	16m 44s
While nut carrying, it stopped digging and demonstrated vigilance behaviour.	16m 49s
It then dug another hole.	17m 01s
Moving to a locating 1m from the base of a tree, it appeared to cache the nut at 1m from the tree, facing toward the tree trunk and NE cardinal direction: a hole was dug in the ground, the squirrel then made the typical thrusting action directed toward the cavity, covered it with soil and patted the ground above down. However the squirrel then moved 1m away from area so that it was now 0m from the tree and it still had the nut in its mouth.	17m 07s
It ran up a tree with the nut in its mouth.	17m 24s
The focal squirrel then descended the tree and dug 2 holes at its base.	17m 47s
It stopped digging behaviour and was vigilant to a rook call.	18m 05s
It then began manipulating the nut in his mouth and paws, sometimes appearing to nibble it.	18m 22s
Current behaviour ended and it was vigilant instead.	18m 55s
It then repeated nut manipulation behaviour.	19m 06s
Finally the squirrel made a true cache, facing the tree, in a NE direction, and at 1/2m from the tree but 2m away from where the 'deceptive' cache had been made (i.e., on the opposite side of the tree).	19m 29s
The squirrel then sat on the same gravestone above the cache that was just made, approximately 1/2m away from it, and was vigilant.	19m 38s
It then ran away while being vigilant and went out of sight at 21min 29sec.	21m 29s

Discussion

We found a strong effect of time-period on foraging and vigilance durations. During the period when the stimulus was being played, there was a decrease in foraging and an increase in vigilance during the call. In particular, squirrels displayed more vigilance and less foraging when exposed to predator playbacks compared to the control white noise playbacks. We also found significant differences between latencies to resume foraging depending upon which call was played. Squirrels exposed to the predator playback took longer to resume foraging after the playback compared to the corvid and conspecific conditions to which squirrels responded similarly, taking longer to resume foraging than those squirrels in the control condition who scarcely responded to the playback.

Overall our results show that grey squirrels responded to the playbacks of corvids and conspecifics similarly by displaying alert behaviour when the calls were played and delayed recommencing their foraging behaviour after the calls had ceased. This supports the hypothesis that squirrels respond to these social risks as sources of potential antagonistic encounters, acting in ways that increase their ability to monitor their surroundings by pausing their foraging behaviour. Likewise, squirrels responded to predator calls by increasing the time they were engaged in alert behaviour during the playback, which was performed at a cost to foraging which is as predicted. However, our study shows that although the different cues of risk had similar disruptive effects on foraging for the three experimental playbacks, there were differences in degree of response, with predatory cues bringing about longer disruption to foraging than social cues.

Foraging among competitors

Previous studies demonstrate that while there are benefits to social foraging (reviewed in Galef & Giraldeau 2001), for an asocial species like the grey squirrel (Koprowski 1996) there are a number of costs associated with foraging near either conspecifics or heterospecifics who use the same resources. The increased competition for resources fosters a need to spend more time foraging (Pravosudov & Lucas 2000), and the potential for agonistic encounters encourages more vigilance behaviour (Tarigan 1994), but is performed at a cost to foraging (Makowska & Kramer 2007; Shonfield 2011). Our study clarifies how grey squirrels respond to potential sources of competition while foraging. In response to the risks of both types of social cue, squirrels predominately acted in ways that indicated they viewed the calls of other squirrels and corvids as worthy of caution, as opposed to a signal of increased foraging competition. Future studies could also incorporate the playbacksof calls of other animals in order to assess if they respond similarly.

The effect of the playback upon foraging was not prolonged: after the playback had ended squirrels re-started foraging in an average of 12 seconds for conspecifics and 15 seconds for heterospecific competitors. It seems that squirrels benefit by being wary of nearby competitors, but resume foraging soon after the threat of competition ceases. It is reasonable that squirrels should not remain disturbed for an extended period after the auditory risk has ceased, as it is more profitable for them to maintain a consistently high level of foraging than engage in occasional bouts of vigilance after exposure to a risk cue. In particular, there may be high costs associated with reduced foraging at a time of year when squirrels are increasingly busy caching food for the approaching winter months. However, it is possible that alert behaviours would extend for a longer period of time at other times of year when the associated foraging costs are not as high.

Corvids share similar resources with squirrels and are also known to pilfer their caches (Vernelli 2013). However, based upon the past literature it was unclear how squirrels would react to the corvid playbacks because the results are difficult to compare among the studies that have examined whether grey squirrels are sensitive to corvid presence. Leaver et al. (2007) report that squirrels do not change their behaviour while caching in the presence of corvids, while Schmidt and Ostfeld (2008) report that they do alter their behaviour when recovering food that was buried in the presence of corvids. Our current study provides evidence that squirrels are sensitive to the auditory presence of corvids that compete with squirrels for food resources. Furthermore, they respond to corvid vocalisations in a similar manner to the alarm calls of conspecifics while foraging. A recent study has found that grey squirrels are responsive to alarm calls made by passerine species if they are acoustically similar to squirrel calls (Getschow et al. 2013). However, in our study the corvid calls were not alarm calls but instead contact calls directed at other birds. Corvids vocalising to one another could pose an aggressive hazard to a lone foraging squirrel; they are often larger than grey squirrels, and frequently forage with other corvids for the same resources as squirrels. Thus it seems adaptive that the squirrels respond by engaging in alert behaviour temporarily until the threat has passed. The specific risk which corvids pose to squirrels, whether as competitors for food, cache thieves, sources of aggression, or all three, is still open to more investigation, but our current study highlights that further research in this area would be valuable in order to more fully understand interspecific foraging competition.

Foraging among competitors and predators

Our study also contributes to the existing literature of how predation risk affects the foraging behaviour of grey squirrels. When under increased perceived risk of predation grey squirrels engage in more vigilance behaviour (Partan et al 2010; Partan et al. 2009), which incurs a cost to the amount of time spent foraging (Brown et al. 1992; Makowska & Kramer 2007; Shonfield 2011). In addition, because we have isolated responses to social and predatory risk cues, our study directly compares the contribution that each of these make to overall foraging decisions. Previous research has shown that while some individuals preferentially forage and eat in areas closer to safety (Booth, et al. 2012; Bowers et a. 1993; Brown et al. 1992; Kilpatrick 2003; Lima & Valone 1986; Lima et al. 1985; Newman et al. 1988), some will forage or cache in locations more exposed to predators when the risk of competition is high (Ekman 1987; Koivula et al., 1994; Lahti et al. 1998; Steele et al. 2014). In the current study we have shown that squirrels responded similarly to both predatory and social cues by interrupting their foraging behaviour and engaging in alert behaviours, social cues had less enduring disruptive effects to foraging than the predator cues. This could be partly because the presence of foraging competitors reduces the cost of defence against predators. Indeed it has been shown that squirrels will monitor alarm calls of both competing conspecifics and heterospecifics and change their vigilance behaviour accordingly (Partan et al.

2010; Partan et al. 2009; Randler 2006a; Schmidt et al. 2008). Thus being alert to calls of competitors reduces the need for sustained vigilance to calls of predators. Nevertheless, in an environment where all three cues of risk would be present it is likely that squirrels would be more tolerant to nearby heterospecifics and conspecifics despite their potential disruptive effects to foraging.

There is a possibility that our conspecific playback stimuli could be signalling predation risk. Squirrels communicate through a variety of means (auditory, Horwich, 1972; Lishak, 1982; Lishak, 1984; olfactory, Taylor, 1977; visual, Thompson, 1978) yet most of their communication tends to relate to aggression or threatening conditions (Clark, 2005; Horwich 1972; Gurnell 1987; Steele & Koprowski, 2001) and is primarily used for resource guarding (Thompson, 1978), during mating (Thompson, 1977) and as predator alerts directed at both other squirrels and the predator itself (Lishak, 1984), particularly tail signals and vocalisations (Partan et al. 2009; Partan et al. 2010). The vocalisations used in our study were combination “kuk” and “quaa” alarm calls (Horwich 1972; Lishak 1984). Previous research has suggested that such alarm signals are more likely to be displayed when conspecifics are present (Partan et al. 2010) and therefore our playbacks could be signalling the risk of conflict with another squirrel, but it is possible that they may also signal predator presence. However, it is not currently known whether there are subtle differences in the nature of calls when directed at a conspecific or otherwise. If subjects were responding to conspecific calls as predator alerts then we might expect a similar response to the conspecific playback as to the predator playback. Our results demonstrate that this is not the case; the conspecific vocalisations appear to present a lesser risk than those of the predator calls. Squirrels reacted to conspecific calls by interrupting foraging to a lesser degree than when they heard a predator call, and this suggests that the response is associated with avoidance of intraspecific conflict rather than cue of predation

Incident of ‘deceptive’ caching

A final observation that has not yet been discussed is that of our systematic recording of the possible “deceptive caching” event. Steele et al. (2008) are the only researchers to describe this behaviour, which is similar to a ‘normal caching’ event in most respects, except during ‘deceptive caching’ the individual does not deposit any food in the cache. Steele et al reported the behaviour occurring between 13.2 – 22.3% out of 255 caching events across two sites and two seasons. They describe how this type of behaviour occurred more often in the close presence of conspecifics and after being pilfered by a human, and therefore they suggest that squirrels may do this to deceive those individuals that are watching in order to reduce the risk of cache pilferage. Our current study is the first, to our knowledge, to report this behaviour in an individual outside the two populations observed by Steele and colleagues. Furthermore, this specific type of behaviour has not been observed in similar studies of grey squirrels (Hopewell & Leaver 2008). However, due to the rarity of it in the scientific literature, the behaviour does not appear to be a widespread strategy used by grey squirrels as part of their daily food storing activities.

Conclusion

This study has shown that squirrels respond differently to cues of predation than to cues of conspecific and heterospecific presence, illustrating how they pose different risks to foraging. Squirrels respond to these different cues of risk by demonstrating alert behaviour and limiting their foraging. The perceived presence of competitor species appears to have short-term disruptive affects upon foraging, rather than facilitating it, suggesting that these calls may signal sources of inter- and intra-specific conflict. Foraging is disturbed for a greater length of time after predator calls because of more time engaged in alert behaviour when potential predators could be around. Overall, these behavioural changes are somewhat short-lived, possibly indicating that there are high costs associated with reduced foraging.

Chapter 7: General discussion

Overview: foraging in the face of risks

The aim of this thesis was to explore how grey squirrels respond to different risks in relation to their foraging and food hoarding behaviours, and which factors were associated with cache pilferage behaviour. A series of five studies were conducted across laboratory and field conditions to examine the contribution of competition, pilferage risk and predation risk upon foraging, caching and pilfering. Each study combined various aspects of these factors in order to determine how they affected behaviour. Some studies focussed on squirrels as cachers, others on them as pilferers. The next section will discuss each of these factors in relation to conclusions which can be drawn from the studies presented in this thesis. Following this, some methodological considerations will be presented; some of the difficulties that were faced while investigating these topics will be discussed, including ways that future research could overcome them, alongside ideas to further research in this area.

Foraging competition

Previous research has indicated that there are costs and benefits to social foraging: foraging neighbours limit the availability of resources as well as acting as a direct source of potential conflict because competitors feed from the same patch (Gerber et al. 2014); nevertheless foraging alongside others can be less costly than foraging alone because of the benefits of being at reduced risk of predation (Verdolin 2006). Two field studies were carried out to investigate how competition from conspecifics and heterospecifics affected foraging and caching behaviour in grey squirrels.

Intraspecific competition

Grey squirrels are considered to be asocial but they also frequently forage alongside conspecifics who share the same food patch (Koprowski 1996). Foraging in a social environment can be adaptive because *individuals* have less chance of being targeted through the dilution effect and they do not need to visually scan for predators as often, so can spend less time being vigilant and more time foraging (Lima 1995). This thesis presents two studies indicating that squirrels are averse to social environments, and thus may not benefit from social foraging. Chapter 6 illustrated that the auditory presence of conspecifics resulted in squirrels increasing their time spent being vigilant, which lessened the amount of time they spent foraging, and also that they took longer to resume foraging when exposed to calls of squirrels in comparison to a control playback stimulus. Data in Chapter 4 shows that squirrels were attentive to conspecifics while foraging and acted in ways to minimise contact with them; the presence of a more dominant conspecific minimised other squirrels' access to the provisioned food source, and while storing food individuals engaged in behaviour that allowed them to more easily respond to competition; for example, caching squirrels would be more likely to orient towards conspecifics when they were closer to them or in areas high in foraging competition. Previous research has indicated that grey squirrels are sensitive to conspecific presence while foraging and modify their behaviour in different ways; for example, they will transport food away from locations high in conspecific density (Hopewell et al. 2008; Spritzer & Brazeau 2003), and engage in alarm (Partan et al. 2009; Partan et al. 2010) and vigilance behaviours (Tarigan 1994) in response to conspecific cues. In combination the results from this thesis suggest that the social environment imposes risks for foraging grey squirrels that necessitate increased vigilance and forestalls food access. This supports the idea that squirrels respond to conspecifics as sources of antagonistic encounters, acting in ways that limit the possibility of interaction, as opposed to viewing conspecifics as competitors for resources, in which case they would be more likely to increase their foraging efforts.

Interspecific competition

Complex relationships can exist between heterospecific competitors across different food hoarding species (e.g., Leaver & Daly 2001), though it is a topic that has received very little research attention. The data in Chapter 6 reported that squirrels responded similarly to the calls of conspecifics as they did competitor heterospecific species in terms of foraging and vigilance behaviours. Whether grey squirrels responded to corvids as competitors while foraging had not previously been investigated, and the findings were ambiguous as to whether they responded to them as potential cache pilferers. Chapter 6 helps to clarify that corvids may be viewed as a potential source of negative interaction as opposed to competitors for resources, since foraging effort decreased after exposure to playbacks of corvid vocalisations. Given that the presence of heterospecific competitors necessitates increased vigilance while foraging, these findings might help to explain why Leaver et al. (2007) reported that squirrels did not orient themselves away from corvids while hoarding food, and that Schmidt and Ostfeld (2008) found that squirrels reduced their foraging effort while recovering food that had been buried in locations where corvid calls were played. Further research is needed on the effect that heterospecific competitors have upon grey squirrel foraging, particularly corvids as they are known to steal the caches of squirrels and might use OSM while doing so. When studies are carried out examining the behaviour of wild squirrels in response to conspecifics, measuring the presence of heterospecifics could easily be incorporated into designs and might help to reveal a lot more about this relationship.

Pilferage risk

The literature in this thesis illustrates the wide range of research that has been carried out with corvids on the topic of cache pilferage. A large number of studies have experimentally investigated in the laboratory the specific behaviour in which hoarders engage to reduce the risk of cache loss to thieves, and a few have also explored how actual pilferage is achieved. Field observations had revealed that squirrels might behave in a similar way to corvids when storing food (Hopewell & Leaver, Hopewell et al. 2008; Leaver et al. 2007; Steele et al. 2008), and one anecdotal observation indicated that cache loss from conspecific observers was a risk in squirrels (Steele et al. 2014). A laboratory study, presented in Chapter 2 experimentally investigated whether grey squirrels used social cues to assess pilferage risk, and a field study in Chapter 4 explored whether relative dominance status also affected cache decision making. Following on from this, cache theft was investigated from the perspective of the pilferer, as opposed to the cacher, in a laboratory (Chapter 3) and a field experiment (Chapter 5) that both tested what cues are used by thieves when pilfering caches.

Cues used to assess pilferage risk: pilferage experience, conspecific presence, and dominance

Field research had indicated that grey squirrels respond to conspecific audiences when storing food in ways that might help to minimise cache theft, though the precise reasons for this are unclear. Chapter 2 presents data from the first controlled laboratory study of audience and pilferage effects upon grey squirrels. Data show that grey squirrels directly respond to conspecific presence as an indicator of pilferage risk and modify their food hoarding behaviour in ways that reduce the possibilities of pilferage; for instance, when observed by a conspecific squirrels would cache more quickly, make fewer caches, and recover more of their caches. Squirrels also responded to experience of cache loss, but this encouraged them to start eating sooner and eating a greater number of nuts, as opposed to modifying their caching behaviour. This supports what has been reported in field studies (Hopewell & Leaver, Hopewell et al. 2008; Leaver et al. 2007; Steele et al. 2008), as well as clarifying that squirrels are not simply responding to experience of theft of their caches but also respond to social cues.

Previous studies with corvids indicate that scrub jays and Eurasian jays (two species much studied in terms of their caching behaviour) were sensitive to the social conditions at the time caching in terms of relative dominance of the observing individual (e.g., Dally, Emery et al. 2006; Shaw & Clayton 2012a). This was not possible to replicate in the laboratory owing to the difficulties of establishing dominance networks among a captive population, therefore a wild population of squirrels was studied to determine whether dominance played a role in caching behaviour. Data presented in Chapter 4 shows that dominance had an impact upon individuals’ access to resources, which supports previous research that squirrels use their dominance to monopolise food supplies (e.g., Allen & Aspey 1986), but no individual differences in caching behaviour were found in respect of strategies to reduce pilferage. However, as the dominance network in the focal population was very different from what previous research had found in grey squirrels, it was uncertain whether dominance would affect food hoarding behaviour in a situation when the more often reported linear hierarchy was found.

Finally, one study by Steele et al. (2008) had reported frequent occurrences of a behaviour among two different observation sites which they referred to as “deceptive caching”. This behaviour has never been observed outside of the populations described by Steele and colleagues, and thus it was thought that it might be unique to native Eastern grey squirrels inhabiting the USA. The squirrels used in all of the studies of this thesis were Eastern grey squirrels residing in UK to which they are not native. Throughout all laboratory and field behavioural investigations in this thesis a conscious effort was made to detail any incidents of “deceptive caching”. Chapter 6 reports the only systematic observation of the behaviour witnessed in one wild squirrel which conforms to the description provided by Steele et al. Therefore “deceptive caching” might not be something that is limited to native grey squirrels but might also be used, albeit infrequently, by grey squirrels residing in the UK. There could also be an alternative explanation for the behaviour reported in Chapter 6 which is still consistent with Steele et al.’s observations: it is possible that squirrels might be swapping an existing cached nut for a new nut as opposed to making an empty cache (Hempel de Ibarra, personal communication), because the point at which the swap occurs would be unseen (i.e., when the squirrel’s head is below ground level). It is not possible to state with any certainty that “cache swapping” rather than “empty caching” is occurring, but it does provide a more parsimonious explanation for the behaviour observed; indeed “deceptive” caching among the corvid literature is associated with more complex cognition which we do not know if squirrels possess. It is also possible that the behaviour might even serve a deceptive function without squirrels intending it to; whether they are making an empty cache or swapping a nut, the same function would be served. Perhaps a more precise definition of the behaviour is required, or more rigorous observation techniques could be used with populations where the behaviour is seen more frequently, such as using video cameras so that behaviour can be analysed more closely.

How pilferage is achieved: social and visual cues

Pilfering of stored food is common across scatter hoarding species. For cache protection strategies that are used in audience situations to be adaptive, an observer must pose a risk to the caching individual. In some species, pilferage can be achieved at the time of caching, for instance by a more dominant individual supplanting a subordinate while they are caching (however, this is not something that was witnessed in squirrels while collecting data for Chapter 4). Given that squirrels were sensitive to social cues in the study presented in Chapter 2, it was logical to then explore whether the presence of conspecifics was in fact a risk to caching squirrels. Pilferage reduction behaviours reported in corvids have been attributed to some species being able to remember the locations of caches they observed made by another bird (e.g., Watanabe & Clayton 2007). Returning to pilfer a cache after the owner has left the vicinity provides a more adaptive pilferage strategy than immediate theft pilfering a cache because there is less risk posed by the cache owner still being close by. It was investigated whether grey squirrels could use OSM to pilfer caches they had observed another squirrel make. The study in Chapter 3 found no evidence for squirrels using OSM to engage in cache pilferage, and squirrels were slightly more accurate (though not significantly so) at recovering caches they had not seen being made in comparison to those they had witnessed. Therefore, it is unlikely that squirrels engage in pilferage reduction behaviour for the same reasons suggested in some corvid species, principally OSM and sophisticated cognition; instead pilferage reduction behaviours are likely to be a behavioural response to conspecific presence providing a cue of pilferage risk.

Given that squirrels were not using OSM, it was important to explore what other strategies might have use to increase their encounter rate with caches that they had not witnessed being made. Previous studies had reported that caches placed close to the bases of trees had high rates of theft compared to those placed farther away (e.g., Steele et al. 2014), but it was unclear why this might be. The study presented in Chapter 5 used artificial caches made at different landmarks that varied in their exposure to predators and also their food availability; this could help to determine if these factors had an impact upon cache theft given that it is more likely that squirrels would forage in locations higher in food availability and lower in predation risk, as well as indicating whether landmarks could be used by pilferers to locate caches. No evidence was found for a pilferage strategy based upon food availability, but there did appear to be an increase in the rate of cache theft in the springtime at man-made landmarks, in comparison to the autumn where caches were more likely to be pilfered from trees; this will be discussed later in more detail in relation to pilferage and predation risks. Though this research does not explain how pilferers are actually locating caches and whether landmarks are used as beacons to pilfer, it does illustrate where and when pilferage is more likely to occur. Further studies are recommended to specifically test the hypothesis that trees and man-made landmarks might be used as beacons in food retrieval and pilferage by grey squirrels.

Predation risk

In wild animals, deciding where to forage, cache or pilfer is not a simple decision based upon an isolated cue as it can be in laboratory studies. Wild individuals are presented with an abundant amount of information that affects where and when they choose to forage. Predation risk has considerable influence on foraging decisions but is rarely investigated in relation to other risks such as those presented by competitors. Three field studies presented in Chapters 4, 5 and 6 investigated how predation risk was incorporated into foraging, hoarding and pilferage decisions, in relation to the risks that competitors pose both to caches and while foraging.

Predation risk in relation to general foraging

An abundant amount of research shows that foragers are sensitive to cues of predation (reviewed in Verdolin 2006). Typically studies of grey squirrels measure foraging distance from refuge as an assay of predation risk, though few studies have investigated how foraging behaviour is modified in response to specific cues of predation. Chapter 6 includes data from a study which presented auditory playbacks to wild foraging grey squirrels in order to measure how foraging behaviour was affected by the perceived presence of predator species. Predator playbacks were consistently found to increase vigilance behaviour and decreased foraging behaviour, and individuals did not resume foraging for an average of 100 seconds after the playback. The effect of competitor playbacks on foraging behaviour also produced a similar outcome though responses were less enduring than to the predator playbacks. Some researchers consider grey squirrel vocalisations to act as cues of predation risk because they are directed toward predators, as opposed to toward conspecifics (discussed in Partan et al. 2009; Partan et al. 2010), though this not been experimentally investigated. Nevertheless, these results highlight the disruption that predatory cues have upon foraging which reflects how the risk that predation disturbs foraging more than the risk of competition, or indeed cues of predation by conspecifics.

Predation risk in relation to cache placement

Foraging distance to refuge has been used as a measure of predation assessment in several previous studies of grey squirrels, with individuals opting to forage or consume food in locations closer to trees (e.g., Lima & Valone 1986; Lima et al 1985). Cache placement relative to predation risk is less understood, with a recent study by Steele et al. (2014) reporting that grey squirrels prefer to place favourable items in locations more exposed to predators because it reduces the risk of pilferage. Chapter 4 measured the distance squirrels placed their caches from trees and found they placed nuts an average of 2.61m away from the base of trees, but this was not related to any pilferage reduction behaviours (dominance, curtailed digging, use of visual barriers, or caching orientation). It is possible that the choice of observation site with a large percentage of canopy cover gave too much protection from predation risk relative to the other measures, as squirrels will naturally forage where there is more canopy cover. In addition, simply using observational data to measure willingness to expose oneself to predation may not be a suitable way to measure the behaviour. Instead, experimental field methods seem to reveal more about how behaviour changes in response to changes in risk, with manipulations such as placing food in different locations that vary in exposure to predators (e.g., Newman, et al. 1988), or using predator cues like the study presented in Chapter 6.

Predation risk in relation to pilferage risk

Finally, the relationship between cache pilferage and predation risk was explored, from the perspective of the pilferer in terms of where would be the optimal location to forage and to thieve caches, and from the perspective of the cacher in terms of the optimal location to ensure cache longevity. Previous studies had reported that grey squirrels chose to cache more favourable items away from trees (Steele et al. 2014). It was suggested by Steele and colleagues that this was because trees provided safer locations to forage for naive pilferers as well as an escape route from predators. However, this may not be the reason for cachers' preferences; rather trees might simply have more foragers around them because they provide a source of food. Chapter 5 presents data that experimentally investigated these different hypotheses at four different types of landmark that varied in predation risk and food availability. This study found no differences in pilferage rates of caches in terms of food availability, but there was difference in pilferage rates between the autumn and spring in locations that varied in predation risk. The finding that pilferage rates were higher in areas low in predation risk in the autumn, i.e., trees, supports the suggestion of previous researchers; that individuals are more likely to encounter caches while foraging in locations that provide safety from predators (Stapanian & Smith 1978; 1986; Steele et al. 2014). With regards to pilferage in the spring, it was suggested that the mediating effect of season could be due to seasonal differences in food availability. It was suggested that in the spring there are generally fewer caches available and therefore pilferers are more likely to forage away from safety, in comparison to the autumn when there are an abundance of caches being made. This is supported by Thompson (1978) who found that in the spring grey squirrel foraging activity peaked and home range size increased, which is suggested to be as a result of food shortage at this time of year. Researchers tend to not study caching-related behaviours in squirrels outside of the peak autumn caching period, however, the results from Chapter 5 indicate that it would be worth investigating further. Field observations carried out across different seasons of where squirrels forage relative to trees would help to clarify if there are any differences in aversion to predation risk as a function of seasonal food availability.

A note on foraging cognition

Among the corvid literature, it is thought that many of the behaviour in which they engage while caching and pilfering might be due to their sophisticated cognitive abilities (reviewed in Clayton et al. 2007 and Grodzinski & Clayton 2010). The data in Chapter 2 supports research on wild squirrels which shows that, like corvids, squirrels engage in pilferage reduction behaviour in response to conspecific presence (Hopewell & Leaver 2008; Hopewell et al. 2008; Leaver et al. 2007; Steele et al. 2008). However, when looking at squirrel foraging, caching and pilfering behaviour more broadly from the data presented in this thesis, the mechanisms for behaviour reported in corvids are likely to be different of that in squirrels. It seems that grey squirrels simply respond to immediate risks in their environment and change their behaviour accordingly depending upon the costs and benefits; using strategies that have evolved because they help to minimise the costs of foraging and hoarding when exposed to cues of risk. The behaviours in which corvids engage while storing food are suggested to be more sophisticated tools that serve to deprive competitors of information, which is linked to complex cognition such as mental attribution (Grodzinski & Clayton 2010). That squirrels simply modify their behaviour in response to cues of risk provides a more parsimonious explanation for the way that they behave. However, there is still the potential for future research to be conducted to establish whether squirrels are sensitive an observers point of view while caching, like in corvids. Overall, this thesis helps to elucidate previous research on grey squirrels that investigated whether some of their behavioural strategies might be related to more complex cognition (discussed in Hopewell 2008).

Summary: foraging in the face of risks

This thesis has shown how different risks affect grey squirrel foraging and hoarding behaviour; a variety of field and laboratory studies have manipulated cues of risk in relation to competition from heterospecifics, conspecific presence and dominance rank, pilferage risk and experience, and predation.

Grey squirrels were found to respond to conspecifics as cues of risk while foraging and caching, and they modified their behaviour in ways that helped them to keep track of their presence, for example, facing toward them, and engaging in vigilance. When storing food, squirrels responded to conspecific presence by adjusting their caching behaviour in ways that might help to minimise pilferage. They were also vigilant of competing heterospecific species, namely vocalisations of corvids, which indicated that heterospecifics were regarded as a risk more than as a competitor for resources.

Cache pilferage was apparent in locations where grey squirrels were observed. Pilferage rates were not uniform across locations or seasons, instead some caches were more likely to be stolen from than others. Pilferage was higher in the autumn when squirrels spend more time foraging for nuts to bury, than compared to the spring. Predation risk also fed into foraging decisions and impacted upon cache pilferage rates in two ways. Firstly, in terms of pilferage rates, in the springtime when there were fewer caches to recover, pilferage rates were higher in areas more exposed to predators, indicating that squirrels were less averse to predation risk when there were fewer resources to forage. Secondly, predator cues were found to be disruptive to squirrel foraging because of the need to spend more time being vigilant.

Overall each of these factors were found to disrupt grey squirrel foraging and/or caching behaviour to different degrees. When combining the results of the studies in this thesis, squirrels seem to be most affected by predatory cues while foraging, and wary of competitors because they might pose a risk to personal safety. In the laboratory where the risk of interacting with a competitor was removed but pilferage risk was high, squirrels responded to conspecifics as though they posed risks to their caches.

Methodological considerations

The studies carried out in this thesis allowed us to examine questions about behavioural responses to risk in both captive and wild grey squirrels. A number of challenges were faced using both laboratory and field methods, some of which have already been outlined in Chapters 2 through 6. The following discussion will re-address some of the issues raised by the methodology, and justify the choice of methods at the time, alongside suggestions for improvements to the methodologies that could be used in future studies.

Laboratory studies

For the study presented in Chapter 2 it was essential that experiments were carried out with captive individuals. Prior research had already indicated a tendency for squirrels to modify their behaviour in response to conspecific and heterospecific presence as well as pilferage, but it was unclear what their separate impacts were upon behaviour. By carrying out a laboratory controlled study these variables could be isolated in order to determine their individual effects, something which cannot be easily achieved in field investigations. Similarly for the study presented in Chapter 3, the nature of the investigation meant that it was necessary to isolate variables so that their individual impacts on behaviour could be assessed, namely olfactory and social cues. By carrying out experiments in a captive situation, procedures could be used that had been tried and tested with other species so that direct comparisons could be made between the results. Furthermore, while some studies have reported OSM anecdotally in wild individuals, it is not something that can be easily (if at all) studied in the field, thus necessitating captive studies.

Nevertheless, there are a number of disadvantages to studying wild behaviour in captive animals. First and foremost, captive environments cannot adequately represent the natural habitat of wild animal in an ecologically realistic way; for example, in terms of the size of arena, social dynamics, challenges and risks faced, among many other aspects. More specifically, for studies that investigate caching behaviour, the costs and benefits of where, when and how individuals forage, cache or pilfer, are not the same for captive animals as for their wild counterparts. While some captive environments do strive to make living conditions appear more natural, such as zoological parks, the conditions necessary to carry out controlled laboratory studies certainly do not, because they seek to control potential extraneous variables. Therefore, while controlling variables allows their effects to be studied in isolation from one another, these measures do not realistically represent how they would appear in wild populations. This may explain why some studies of captive animals do not yield the same results as those conducted with wild individuals; for example, spatial memory in grey squirrels is not always possible to replicate in the laboratory (e.g., Meier, 2011) as it appears in wild squirrels (Macdonald 1996). The squirrels in the current study were motivated to cache all year round, however this has not been true of previous investigations with captive squirrels (Hopewell 2008). Thus, captive individuals might not behave in a way that can be generalised to wild populations. Unfortunately, this is a problem across all studies that attempt to study natural behaviour among captive individuals.

A second problem with using laboratory housed animals is testing a large enough sample size in order for results to be meaningful. As has already been noted in Chapters 2 and 3, using non-domesticated species requires effort to habituate them to captivity and often hand-rearing from a very young age (in the case of grey squirrels, approximately four weeks old in order for them to habituate to humans). These conditions can be difficult to achieve. For grey squirrels in particular, minimum housing requirements can be substantial: most of the time they need to be housed individually; each cage requires adequate materials and space for them to engage in some natural behaviour, and provide adequate psychological and physical stimulation in order to prevent abnormal or damaging behaviour; they are great escape-artists meaning that structurally the cages require maintenance to remain sound; in the UK, as they are a non-native species, housing must be approved by the Home Office and subject to regular inspection; they need frequent positive contact with humans so that they do not become timid and less willing to participate in experiments; and on top of this, the costs of husbandry, food and veterinary care need to be met. Ultimately, meeting these basic needs requires considerable time, space and finances, even to house only a small number of individuals. What is more, there is still a high probability that a number of individuals will not thrive; of the 17 squirrels that were obtained to investigate studies in this thesis, only six individuals were sufficiently habituated and / or survived long enough to participate in studies. It seems that grey squirrels simply do not adjust well to captivity. These reasons might indicate why so few studies have been carried out with captive grey squirrels in the past. Small sample sizes are a common problem across laboratory studies, but nonetheless a large number of studies still reveal interesting results. Furthermore, in spite of the difficulties of faced by studying laboratory housed grey squirrels, two studies in this thesis present valuable data that has helped to further our understanding of grey squirrel caching and pilfering behaviour.

Field studies

In Chapters 2 and 3 the suggestion was made that more naturalistic captive settings should be used to study grey squirrels, such as wildlife sanctuaries that house individuals in large outdoor enclosures. Though variables could not be as easily manipulated and controlled as in laboratory studies, the results from such research would be more ecologically relevant and be more generalizable to wild populations. Nevertheless, where suitable techniques are available it should be preferable to study wild individuals, as a field situation can provide much more ecologically relevant data. The studies presented in Chapters 4 through 6 opted to investigate behaviour in its natural setting. There were two major difficulties with studying grey squirrel behaviour in the field. Firstly, even though samples much larger than in the laboratory were more easily achieved, locating a large enough sample size for a particular experimental design, while minimising pseudoreplication, was still challenging. Secondly, it was difficult to observe enough instances of a desired behaviour when data collection was limited to the peak caching season, a period of three months each year. For these reasons, three different methodologies were applied depending upon the questions being asked, which attempted to overcome these difficulties. Each of these methodologies addressed these problems in different ways, as will now be discussed.

For the first field study (presented in Chapter 4) it was necessary that we measure a dominance network so that this could be used to determine whether there were differences between high and low ranking individuals in terms of their caching decisions. This meant that multiple behavioural events needed to be recorded for individual squirrels to determine whether their behaviour was consistent over time. Therefore data collection was focussed to one location to measure the behaviour of one population of squirrels; marking individuals avoided the possibility of pseudoreplication. The observation site was provisioned with nuts to ensure that enough behavioural interactions were witnessed to measure dominance, and enough instances of caching behaviour were included in the data during the limited data collection period. While these methods were necessary for the study design, they presented several problems. Though traps were placed in and surrounding the study site in order to mark squirrels for identification purposes, an unknown number of unmarked individuals contributed to the data. Unfortunately this is always going to be a difficulty when opting for this method; some individuals may never be trapped and marked, and then consequently there is the decision of how to handle the data from unmarked individuals. Trapping and marking can also be quite time consuming, which needs to be traded-off against time that could be spent making behavioural observations, and it restricts data collection to locations in which trapping has been successful. Nevertheless, this method can yield a lot of behavioural data about a small number of individuals, which can be a useful design for some types of research question. Provisioning food in one central location meant that a large number of behavioural interactions were recorded which helped to build a social network based upon dominance, as well as also measuring a large number of caches made out of the provisioned food. Unfortunately, the provisioning probably did result in an unexpected tyrannical hierarchy, perhaps because receiving a large amount of food in this manner is not a frequent natural occurrence. This meant that although interesting conclusions could be drawn about caching behaviour in general, it was more difficult to do this in relation to dominance behaviour. Data collected from provisioning methods is definitely enhanced in terms of quantity (it is unlikely that enough interactions or natural caches would have been witnessed without it), but provisioning is a method that should be used with caution depending upon the behavioural questions being asked.

A different data collection method was used in the field behavioural study presented in Chapter 6. In this study the problems associated with marking squirrels at one location were avoided, as well as still managing to avoid pseudoreplication; only one squirrel was observed at each site visited. Obviously, it may not always be feasible to use this method (for example as with the study presented in Chapter 4, or in general with any study where repeated measurements of individuals are required). It can also be time consuming and costly to get to a large enough number of sites, and there is no guarantee of collecting the data that you need on each visit. However, the advantages of using this data collection method far outweigh the costs, and where possible I would advocate using this method to observe behaviour in squirrels. Sample size is virtually limitless because it simply depends on how many can be visited in one caching season. Appendix D provides a list of locations across South and East Devon that were used in Chapter 6 and could be used to speed up the research process for future investigators wanting to use this method to collect behavioural data on squirrels.

One consideration worth bearing in mind before setting out to collect data in this manner, concerns whether using this method will generate enough data. As already noted there is a difficulty of witnessing enough of a particular behaviour because data collection on squirrel foraging is typically limited to the autumn months. Indeed, the data collected for Chapter 6 had originally included caching behaviour but not enough instances were witnessed in order to include it in the study. Therefore, it is suggest that combining the methods used in the studies of Chapters 4 and 6 might help to overcome this problem; principally, that provisioning is used but across multiple locations, observing only one focal animal at each site. However, instead of provisioning as a bonanza, it would be preferable (and more ecologically valid) to use less food and scatter it across an observation site to increase the number of caches witnessed. Using such a method presents the focal animals with a foraging situation that is much more familiar, not simply from food dropped by trees, but also from people who visit parkland to feed animals.

A third approach was used in Chapter 5, namely measuring the pilferage rates of experimenter-made artificial caches, a method used in a large number of studies within the literature. The biggest limiting factor of this study is locating a suitable area where it can be carried out; a location that is large enough to provide a number of discrete populations of squirrels, and where permission is granted to make artificial caches. Although, this study design takes a lot of person-hours to conduct, it can yield large data sets, and is certainly a method that would benefit future studies. It is also an appropriate method if assistance from volunteers is available as the techniques require minimal training in behavioural observations. If possible, also using video recorders at each location could monitor the behaviour of the pilfering animals; this would help to further determine how they locate caches, and what is done with the pilfered food. Nevertheless, this could be financially costly and the risks of theft or damage to equipment in public locations could be high.

Future directions

This thesis has helped to clarify what cues grey squirrels are sensitive to when making caches; specifically, that squirrels primarily respond to the presence of conspecifics when making food hoarding decisions. Considerably more studies have been carried out with food hoarding corvids to further identify mechanisms that might be involved in these behaviour. Not only do corvids respond to the mere presence of conspecifics as potential pilferers, but when presented with the opportunity to store food in locations with less visual access to onlookers they preferably cache in these locations (e.g., Dally et al. 2004; Dally et al. 2005). This has been attributed to theory of mind like abilities among some species of corvid, suggesting that they are aware of their observer's point of view when storing food. Studies in the field with grey squirrels indicate that they may behave similarly to corvids; for example, Leaver et al. (2007) report that wild grey squirrels are more likely to cache oriented away from conspecific onlookers. In the laboratory study presented in Chapter 2, this was not found, and in the field study presented Chapter 4 the opposite was found to be the case; however these results could be attributable to the different experimental designs of the studies. For instance, when the caching and the observer squirrel are so close to one another, the cacher may not engage in such behaviour because it would simply not be effective to reduce pilferage, and when a competitor is at closer distances it could even benefit the cacher to monitor their competitors location. It is suggested that further research use a design that has been tried and tested in other laboratory studies to more easily identify how and why squirrels are responding to onlookers. For instance, Dally and colleagues reported that Western scrub jays would hide food in locations that provided more difficult visual access to onlookers, such as in the shade (Dally et al. 2004), or in out of view locations (Dally et al. 2005), regardless of their distance to onlookers. This is something that the current laboratory conditions could be easily adapted to measure. Moreover, now that it has been clarified that squirrels respond to conspecifics as potential immediate pilferers of their caches, this type of study could be conducted in the field; for instance, by providing distinct visual barriers at field sites, scatter-provisioning animals on one side of the barrier and measuring where they prefer to cache. This would help to determine whether squirrels are actually sensitive to conspecifics observing where they cache, or if caching is simply inhibited by their mere presence. Furthermore, by studying the behaviour in the field it would be easy to measure behaviour in response to the presence of heterospecific competitors who also access the provisioned food. Far less is known about heterospecific than conspecific competition across different caching species, though data in this thesis indicates that it does affect foraging behaviour and so it is definitely something that should be incorporated into field studies.

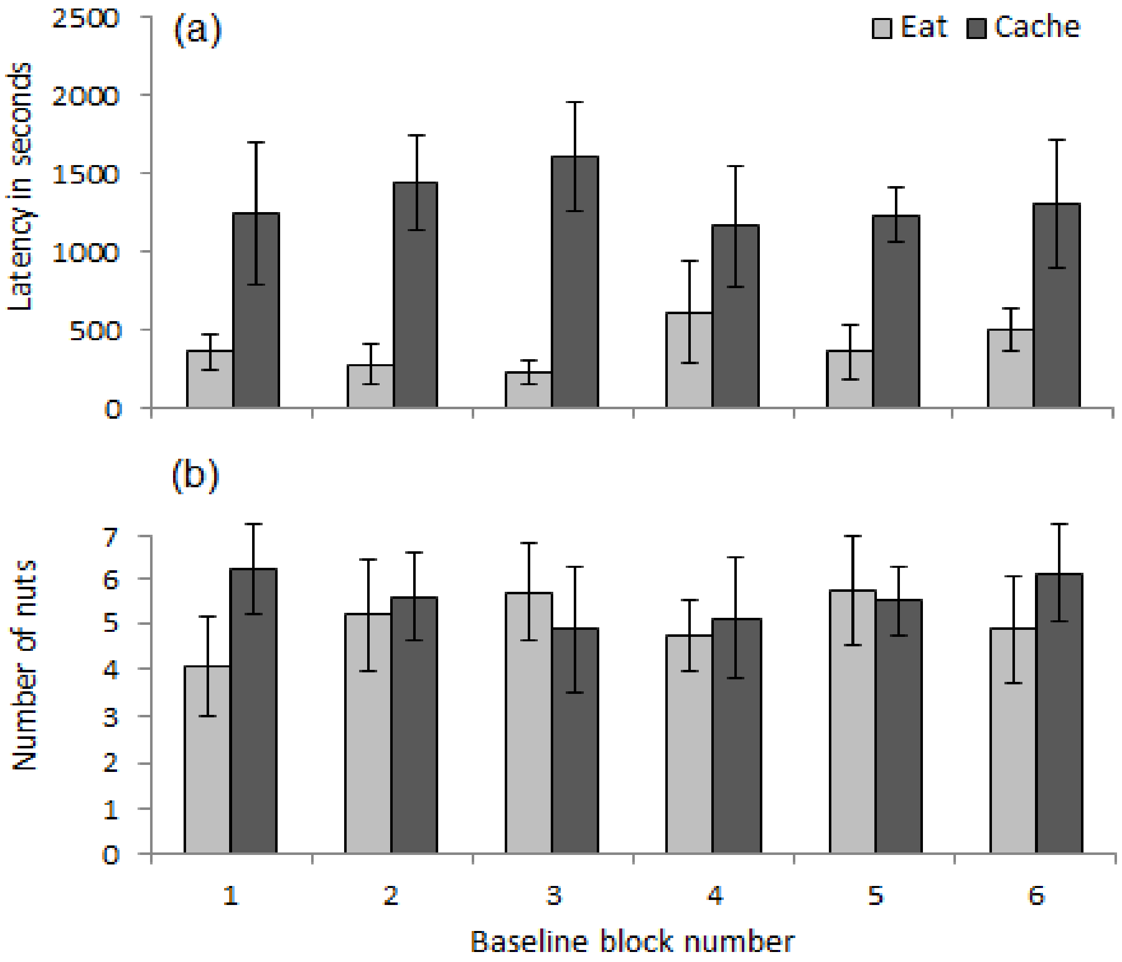
A second major area that is in need of much more research, not only in grey squirrels, but caching animals in general, is how animals pilfer. Some species are sensitive to pilferage, which indicates that pilfering behaviour is a real problem. However, little is known about how pilfering is achieved. This thesis has reviewed some of the strategies that might be used by different species to engage in cache pilfering behaviour, it also presents the first studies conducted with grey squirrels to assess whether they can use OSM to pilfer, or whether they might simply pilfer in optimal foraging locations away from predation and close to food. These studies reveal that squirrels use olfactory cues to locate caches as opposed to OSM, and that pilferage is not achieved by simply foraging in the the most likely foraging locations. However, much more research needed to be carried out in this field to further understand the specific cues used to engage in cache pilfering behaviour. Because it is a much more difficult behaviour to monitor than caching, particularly in field studies, future studies are likely to be within laboratory conditions or to use experimenter-made caches in the field.

Conclusions

The data in thesis has explored how different cues of risk influence foraging, caching and pilfering behaviour in the grey squirrel. Predator cues have been reported to be most disruptive to foraging behaviour in comparison to competitors, but seasonal differences in food availability appears to influence aversion to predation risk when pilfering. Squirrels respond to conspecific and heterospecific competitors in ways that help to avoid potential negative interactions while foraging; and when storing food, squirrels respond directly to conspecifics as sources of risk to their caches. Overall, this thesis helps to clarify results of previous field observations that have been carried out on grey squirrels by incorporating combinations of the different challenges they face while foraging. Some of the findings present new directions that future research should pursue, including the mechanisms that squirrels use to assess pilferage risk in conspecifics, and what cues might be used to aid cache pilferage.

Appendices

Appendix A: For study presented in Chapter 2. For each squirrel one block from the baselines was selected randomly to be used as a control condition. Therefore, we wanted to ensure that are baseline measures provided consistent measures across time. This is displayed for the following measures: (a) Latency to eat and cache across each block. (b) Number of nuts eaten and cached across each block.



Appendix B: For study presented in Chapter 3. Sequence of trials for all four subjects across the three repetitions. Subjects were randomly allocated in terms of laminate position and cage side across the trials.

Key:
Habituation trial 1 = olfactory cues present & visual access available.
Habituation trial 2 = olfactory cues present & visual access available.
Test A = visual access blocked, with olfactory cues & caches present.
Test B = removal of olfactory cues (caches absent), with visual access available.

Trial Description	Day sequence	Repetition	Laminate side	Observer identity	Observer cage	Cacher identity	Cacher cage
Habituation trial 1	1	1	Front	Arnold	Left	Sarah	Right
	2	1	Rear	Leonard	Right	Simon	Left
	3	1	Rear	Sarah	Right	Arnold	Left
	4	1	Front	Simon	Left	Leonard	Right
Habituation trial 2	5	1	Rear	Arnold	Left	Sarah	Right
	6	1	Front	Leonard	Right	Simon	Left
	7	1	Front	Sarah	Right	Arnold	Left
	8	1	Rear	Simon	Left	Leonard	Right
Test A	9	1	Front	Arnold	Left	Sarah	Right
	10	1	Rear	Leonard	Right	Simon	Left
Test B	11	1	Rear	Sarah	Right	Arnold	Left
	12	1	Front	Simon	Left	Leonard	Right
Test B	13	1	Rear	Arnold	Left	Sarah	Right
	14	1	Front	Leonard	Right	Simon	Left
Test A	15	1	Front	Sarah	Right	Arnold	Left
	16	1	Rear	Simon	Left	Leonard	Right
Habituation	1	2	Front	Sarah	Right	Simon	Left

trial 1	2	2	Rear	Arnold	Left	Leonard	Right
	3	2	Rear	Simon	Left	Sarah	Right
	4	2	Front	Leonard	Right	Arnold	Left
Habituation trial 2	5	2	Rear	Sarah	Right	Simon	Left
	6	2	Front	Arnold	Left	Leonard	Right
	7	2	Front	Simon	Left	Sarah	Right
	8	2	Rear	Leonard	Right	Arnold	Left
Test A	9	2	Front	Sarah	Right	Simon	Left
Test B	10	2	Front	Arnold	LH	Leonard	Right
Test A	11	2	Rear	Simon	Left	Sarah	Right
Test B	12	2	Rear	Leonard	Right	Arnold	Left
Test B	13	2	Rear	Sarah	Right	Simon	Left
Test A	14	2	Rear	Arnold	Left	Leonard	Right
Test B	15	2	Front	Simon	Left	Sarah	Right
Test A	16	2	Front	Leonard	Right	Arnold	Left
Habituation trial 1	1	3	Front	Simon	Left	Arnold	Right
	2	3	Rear	Sarah	Right	Leonard	Left
	3	3	Rear	Arnold	Right	Simon	Left
	4	3	Front	Leonard	Left	Sarah	Right
Habituation trial 2	5	3	Rear	Simon	Left	Arnold	Right
	6	3	Front	Sarah	Right	Leonard	Left
	7	3	Front	Arnold	Right	Simon	Left
	8	3	Rear	Leonard	Left	Sarah	Right
Test A	9	3	Rear	Simon	Left	Arnold	Right
Test B	10	3	Front	Sarah	Right	Leonard	Left
Test B	11	3	Front	Arnold	Right	Simon	Left
Test A	12	3	Front	Leonard	Left	Sarah	Right
Test B	13	3	Front	Simon	Left	Arnold	Right

Test A	14	3	Rear	Sarah	Right	Leonard	Left
Test A	15	3	Rear	Arnold	Right	Simon	Left
Test B	16	3	Rear	Leonard	Left	Sarah	Right

Appendix C: For study presented in Chapter 4. A summary of the outcome of GZLMs which measured whether different pilferage avoidance strategies were used as a function of caching distances to pilferage risk, competition and predation. Outcomes correspond with predictions that were made in Table 7. Results show that subjects primarily acted in ways to avoid competition. There were no differences in strategy use depending upon squirrel identity.

Caching distance in relation to risk of…	**Predictors:**		
	Curtailed digs	**Caching orientation**	**Use of visual barrier**
Cache pilferage	One of the best predictors for explaining whether cachers engaged in curtailed digging was caching distance to nearest neighbour. Squirrels made fewer curtailed digs when closer to another squirrel. This is in the opposite direction to what would be predicted in terms of pilferage avoidance.	The best predictor for explaining whether cachers would orientate themselves away from onlookers while caching was distance from another squirrel. Squirrels were more likely to face toward a neighbour when closer to them. This is in the opposite direction of what would be predicted in terms of pilferage avoidance.	Not-significant in the model.
Competitive interaction	One of the best predictors for explaining whether cachers engaged in curtailed digging was caching distance to		Not-significant in the model.

	the food source. Squirrels made fewer curtailed digs when they cached close to the food source. This is in the predicted direction of what would be expected in terms of competition avoidance.		
Predation	Not-significant in the model.	Not-significant in the model.	Not-significant in the model.

Appendix D: List of locations visited during the playback study of Chapter 6 where there was a high density of grey squirrels. Owing to the size of some locations it is possible to conduct more than one observation and still have a good degree of certainty that you are observing a discrete population of squirrels. All locations consist of urban parkland are within a 30 mile radius of the University of Exeter Streatham Campus.

Exeter and surrounding areas
Alphington Church graveyard, Alphington
Bartholomew Cemetery
Bury Meadow Park
Hele Road Church graveyard
Exeter Cathedral
Exeter Cemetery
Northernhay Gardens
Priory Road Park
Quayside parks
Rougemont Gardens
Southernhay Gardens
The Imperial pub beer gardens
University of Exeter Streatham Campus
University of Exeter St Lukes Campus

Exmouth and surrounding areas
Manor Gardens
Phear Park
St Michaels Church graveyard
Woodbury Church graveyard, Woodbury

Newton Abbot and surrounding areas
Ashburton Church graveyard, Ashburton
Bitton Park, Teignmouth
Chudleigh Church graveyard, Chudleigh
Courtney Park
Decoy Country Park

East Park, Teignmouth
Forde Park
Hackney Marshes, Kingsteignton
Kingskerswell Church graveyard, Kingskerswell
Kingsteignton Church graveyard, Kingsteignton
Mill Marsh Park, Bovey Tracey
Stover Country Park, Stover

Paignton and surrounding areas
Oldway Mansion
Preston Park, Preston
Victoria Gardens

Torquay and surrounding areas
Cary Park
Cary Avenue Park
Chapel Woods
Cockington Village Meadow
Cockington Village Ponds
Illsham Road meadow
Meadow opposite Kents Cavern
St Marychurch Church graveyard
Thatcher Rock
The Tessier Gardens
Torre Church graveyard
Torre Abbey Meadows

Totnes and surrounding areas
Berry Pomeroy Castle, Berry Pomeroy
Dartington Gardens
Totnes Castle
Totnes Road Church
Totnes Road Park

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