

Effects of competition and food availability on travel time in scatter-hoarding gray squirrels (*Sciurus carolinensis*)

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Scatter-hoarding animals transport food away from its source before storing it to maximize the likelihood that the cache will survive for use at a later time. However, the more time animals spend transporting and storing the food the less time they have for food collection. Previous studies suggest that the time animals spend on caching depends to some extent on the availability of food and on the presence of conspecifics at the food source. We tested whether a scatter-hoarding mammal responds flexibly to conspecifics as competitors according to the availability of food or if they respond more directly to them as potential pilferers. We used multiple linear regression to model the time eastern gray squirrels (*Sciurus carolinensis*) took to return to nut patches of varying quality after collecting a nut for caching when they were alone and when conspecifics were present. The results provide the first evidence that scatter hoarders respond to conspecifics at a food source primarily as competitors rather than as potential pilferers; the squirrels increased the rate at which they returned to the nut patch when conspecifics were present rather than transport the nuts farther away to minimize the risk of pilferage. In contrast, and in line with previous studies, the squirrels responded to a reduction in the availability of food by increasing the distance at which they stored the food from the source. **Key words:** food competition, gray squirrels (*Sciurus carolinensis*), scatter hoarding. [*Behav Ecol* 19:1143–1149 (2008)]

When an ephemeral source of food becomes available, scatter hoarders maximize the rate at which they store food that survives density-dependent theft by conspecifics (Waite and Reeve 1992a, 1992b). They can do this by caching a volume of food that is large enough to offset loss to pilferers (Dally et al. 2006; Male and Smulders 2007a) or by reducing the likelihood that their caches will be pilfered, for example, by transporting the food away from the source and spacing caches out (fox squirrels, *Sciurus niger*, Stapanian and Smith 1984; magpies, *Pica pica*, Clarkson et al. 1986; Merriam's kangaroo rats, *Dipodomys merriami*, Daly et al. 1992; yellow pine chipmunks, *Tamias amoenus*, Vander Wall 1995) or by delaying caching until there are no conspecifics in the vicinity (willow tits, *Parus montanus*, Lahti and Rytönen 1996; ravens, *Corvus corax*, Bugnyar and Kotrschal 2002). These strategies involve costs: caching at greater distances or after a delay reduces the time available for collecting food, particularly if other foragers are present; dispersing caches more widely increases travel costs; and rapidly hoarding a large volume of food may be energetically costly and involves making caches close to the source where they are most vulnerable to pilferers (gray jays, *Perisoreus canadensis*, Waite and Reeve 1992a; eastern chipmunks, *Tamias striatus*, Clarke and Kramer 1994). Previous studies suggest that whether animals maximize the amount of food they sequester or minimize the likelihood that their caches will be pilfered depends on the presence of conspecifics (see review by Dally et al. 2006), the age or social status of the individual (e.g., eastern chipmunks, Clarke and Kramer 1994; willow tits, Lahti et al. 1998), and on the availability of food (fox squirrels, Stapanian and Smith 1978; magpies, Clarkson et al. 1986; gray jays, Waite and Reeve 1992a).

Studies on how the presence of conspecifics affects the rate at which individuals hoard food have found differing results, suggesting that the exact context in which individuals are caching is important in determining how they should respond. In some studies, hoarders were found to reduce the amount of food they stored when conspecifics were present (willow tits, Lahti and Rytönen 1996; black-capped chickadees, *Poecile atricapillus*, Stone and Baker 1989; coal tits, *Parus ater*, Brotons 2000; scrub jays, *Aphelocoma californica*, Dally et al. 2005) or to travel farther away from the food source before caching (willow tits, Lahti et al. 1998; eastern gray squirrels, *Sciurus carolinensis*, Spritzer and Brazeau 2003; eastern gray squirrels, Leaver et al. 2007). When conspecifics are present, caches made near the source are more vulnerable to pilferers because naive foragers are actively searching for food in the area or, in some species, because conspecifics can observe where caches are being made and use the information to steal the food (anecdotally in kangaroo rats, Daly et al. 1992; nutcrackers, *Nucifraga columbiana*, and Mexican jays, *Aphelocoma ultramarina*, Bednekoff and Balda 1996; ravens, Bugnyar and Kotrschal 2002). In these circumstances, protecting caches from pilferers may be more important than collecting more food. Hoarders may also sequester less food if aggressive individuals prevent them from accessing the source. This is particularly true at rich food patches because they attract more individuals than poorer ones (eastern gray squirrels, Lewis 1980; sparrows, *Passer domesticus*, Johnson et al. 2006) and because dominant individuals are most likely to monopolize the best quality resources (willow tits, Hogstad 1988; Lahti et al. 1998).

In other studies, with captive scatter hoarders, the rate of hoarding was found to increase when conspecifics were present (mice, *Peromyscus leucopus*, Sanchez and Reichman 1987; ravens, Heinrich and Pepper 1998; scrub jays, Emery et al. 2004). In these studies, food was either very limited, creating competition (Heinrich and Pepper 1998), or the conspecific did not have immediate access to the food or any caches being made

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because they were placed in a neighboring cage (Sanchez and Reichman 1987; Emery et al. 2004). These latter studies suggest that in the presence of conspecifics but without the risk of immediate pilferage and only potential competition for food, hoarders responded by collecting more food rather than increasing their effort to protect their caches. It should be beneficial for an individual to sequester a large portion of the food while it has sole access to the source because, for animals that use spatial memory to recover their caches (including eastern gray squirrels, Jacobs and Liman 1991; MacDonald 1997; and chipmunks and many corvids, Vander Wall and Jenkins 2003), the individual that stores the food has an advantage over naive foragers in recovering it (Vander Wall and Jenkins 2003; Vander Wall et al. 2006).

The rate of hoarding when conspecifics are present can also be affected by the extent to which cache protection measures other than transporting food away from the source can be used. For example, larder hoarding rather than scatter hoarding (Merriam's kangaroo rats, Preston and Jacobs 2001), chasing potential pilferers away from caches (eastern chipmunks, Clarke and Kramer 1994), moving vulnerable caches to more secure sites at a later time (heteromyid rodents, Jenkins and Peters 1992; gray jays, Waite and Reeve 1992a; willow tits, Brodin 1994; scrub jays, Emery and Clayton 2001), or using evasive tactics (scrub jays, Emery et al. 2004; eastern gray squirrels, Leaver et al. 2007; Steele et al. 2008) may allow individuals to store more food without significant losses to pilferers.

The presence of conspecifics can also lead to a change in caching behavior independently of any social factors because when they are present and foraging at the same source of food, there is less food available to cache. Models of optimal scatter hoarding predict that hoarders will begin caching quickly, close to the source, but take increasingly longer to return to the food source as it is depleted (Stapanian and Smith 1978; Clarkson et al. 1986; Waite and Reeve 1992a). However, if food is limited from the outset, it cannot be collected and stored quickly and stolen items cannot easily be replaced so storing it securely becomes more important (Longland and Clements 1995; Heinrich and Pepper 1998; Tamura et al. 1999).

We investigated how the way in which scatter hoarders divide their time between making their caches secure and sequestering more food is affected by the presence of conspecifics. The studies discussed previously (Sanchez and Reichman 1987; Clarkson et al. 1986; Waite and Reeve 1992a; Emery et al. 2004) suggest that the effect of conspecifics on caching individuals differs according to whether they are in the vicinity of the food source or elsewhere because they differentially affect the availability of food, competition for food, and the vulnerability of caches to theft. This study focuses only on the effect of conspecifics that are present at a central food source. In a study with eastern chipmunks, individuals were found to be more sensitive to conspecifics as potential pilferers than as competitors at the food source (Clarke and Kramer 1994). Chipmunks generally larder hoard and make caches in the defended zone around their burrows, so if pilferers discover their stored food it could lead to catastrophic loss. In contrast, we expect scatter hoarders to respond to conspecifics that are visiting the same source of food primarily as competitors because for them the loss of food gathering opportunities would be more costly than the loss of one or even several caches.

We recorded the time wild eastern gray squirrels (*S. carolinensis*) spent transporting nuts from artificial nut patches of varying quality when they were foraging alone and compared this with transport times when conspecifics were also visiting the patches. We predicted that, if squirrels respond to con-

specifics as competitors for the nuts, the way in which transport times changed over different food densities would differ between the social and nonsocial conditions. If food is abundant, squirrels can spend time on cache protection measures and return to collect more food in both the social and nonsocial conditions, but when food is scarce, squirrels will have to return more quickly in the social condition because of competition for the food. If, instead, squirrels respond to conspecifics as potential pilferers, we predicted that they would take longer to return to the nut patch in the social than the nonsocial condition for all densities of food because conspecifics represent an increase in the risk of pilferage and aggression at the food source and a reduction in the amount of available food.

METHODS

Observations were carried out at 2 sites, approximately 500 m apart and separated by roads and buildings on the University of Exeter's campus, Devon, UK. Squirrels' caching activity peaks during the autumn, but they store food all year round if available. Observations were made in May and June 2006 (site 1, latitude N50:44:04, longitude W3:32:04) and May–July 2007 (site 2, latitude N50:44:15, longitude W3:32:29). The sites were sufficiently far apart to ensure that we observed different squirrels at each of them. Site 1 consists of approximately 0.6 hectares of parkland scattered with oak and pine trees and bounded on 3 sides by rhododendron bushes, a pond, and a group of pine trees. Site 2 is of similar size on a southwest facing slope with oak, pine, lime, and eucalyptus trees scattered over the area and bound by a road, foot paths, and a car park and buildings at the bottom of the slope.

The squirrels on campus are habituated to human activity and so were easy to observe. Although gray squirrels are diurnal with peaks of activity in the early morning and at dusk, previous studies have found that squirrels on the campus are also active from mid-morning to early afternoon (e.g., MacDonald 1997; Leaver et al. 2007). Observations were made 4–5 days a week between 11:00 AM and 2:30 PM or 4:00–7:00 PM. To attract squirrels to the site, a metal tray containing a mixture of walnuts, pecans, almonds, and hazelnuts (all in shells) was placed on the ground near the center of the sites next to a large tree stump and oak tree (site 1) and a eucalyptus tree (site 2) that squirrels were frequently seen to climb. Observations were made from approximately 20 m away, and a digital video camera was used to film squirrels as they visited the tray. Notes were made on individual squirrels' distinctive markings, tail shape, body size, and typical behaviors. After 3 weeks, 4 squirrels at site 1 (referred to as BL, PL, RT, and NW) regularly visited the tray soon after it was put out. The sex and age of these squirrels were not known, but their size and condition suggested that they were all adults. To test the reliability of identification, 30 still pictures were taken from the video footage, and an independent observer who was inexperienced in identifying wild squirrels was asked to group pictures of the same squirrel together. They agreed with the experimenter on 76.7% (23/30) of the pictures. As the experimenter could also make use of each squirrel's typical behavior for identification and was experienced at identifying squirrels from previous studies, this was taken as an acceptable level of agreement.

At site 2, 13 squirrels were trapped, marked with black hair dye in distinctive patterns on their fur, and released. Trapping was carried out in accordance with ASAB guidelines and under a Natural England permit to live trap and release. The traps were baited with peanut butter, set around the site in sheltered locations and checked every hour to ensure that trapped

squirrels could be marked and released as quickly as possible. Four of these squirrels regularly visited the nut tray within a week (3 adult females, NK, MT, HP, and 1 adult male, SD).

For testing, a piece of thick blue string was used to mark out the nut patch, a circular area of ground (radius 50 cm) including the area where the tray had been. The string was held in place with short twigs (approximately 10 cm) stuck into the ground. The ground inside the circle was covered with leaf litter gathered from around the area. During testing, only intact hazelnuts (*Corylus avellana*) were provided. On the first experimental day, 30 hazelnuts were placed on top of the leaf litter to habituate the squirrels to the nut patch. Data from this experimental day were not used in the analysis. On other experimental days, nuts were mixed into the leaf litter so that they were not necessarily visible on the surface. The number of visible nuts was not controlled except in the 50-nut condition, when the experimenter ensured that at least 10 nuts were on the surface in order to generate some very short search times. On the first day of testing, 30 nuts were mixed into the leaf litter, and this was reduced to 20, 10, and 2 nuts and then increased to 50 nuts over subsequent sessions. The density of nuts presented each day was determined by lottery, with the restrictions that patches on consecutive days were never the same; all 5 densities were presented at least once before being presented again, and, on the last 3 days of the study, patches that had not been visited by some squirrels were chosen again. At the start of the experimental day, the nut patch was set up with the required number of nuts. The first squirrel to visit the patch was usually selected for observation, but less frequently observed squirrels were favored. The focal squirrel was observed continuously until it remained out of view for more than 15 min or the experimenter judged the patch to have been depleted, by keeping track of the number of nuts that had been taken. In both cases, the experimenter checked the patch, counted any remaining nuts, and added more nuts to make up the required number for that day. If the focal squirrel that was being observed before the patch was replenished had not been absent for 15 min and returned in less than approximately 10 min of the experimenter leaving the patch, observations of that squirrel continued. This happened in the 2-, 10-, and 20-nut conditions, where the patch was depleted rapidly (<5 min); in the 2-nut condition, a single focal squirrel visited 2 (3 squirrels), 3 (3 squirrels), or 4 patches (1 squirrel) in one day; in the 10-nut condition some visited 2 (1 squirrel) or 3 (1 squirrel); and in the 20-nut condition, 1 squirrel visited 2 patches. Between 1 and 6 nut patches were presented per day, but in most cases (73/83) each focal squirrel was only observed visiting one patch in a day. If the focal squirrel had gone out of view for more than 15 min, or did not return within 10 min of the patch being replenished, the next, different squirrel to visit the patch was selected for observations. It was not possible to predetermine and equalize the number of presentations of each density for each squirrel as not all squirrels visited the circle every day, but at the end of the study each squirrel had taken nuts from patches of every density on 2 or 3 days. Observations were made on 33 days at site 1 and 34 days at site 2, and all squirrels were focal squirrels on at least 3 of the 4–5 observation days per week.

At the end of the experimental day, any remaining nuts and the string were removed and the leaf litter was collected into a plastic bag for use on the next day.

The following measures were recorded for each visit to the nut patch: the identity of the focal squirrel, the time between it placing at least 1 paw inside the circle and leaving so that all 4 paws were outside the circle (search time), and the number of other squirrels in the nut patch. For all but the last visit of each squirrel in each session the time between leaving and

returning to the nut patch was also recorded (travel time). Travel time included the time squirrels spent transporting a nut, burying it, and disguising the cache. It was not possible to see the squirrel make a cache on every trip as they often traveled under bushes around the edge of the site, so the experimenter noted down whether the nut was stored within view or not. We assumed that squirrels were storing the nuts when they went out of view because, as non central place foragers, when not caching they usually eat their food where they find it, unless there is a risk of predation or aggression from conspecifics. Even then, they carry food to the nearest place of safety, being less likely to transport food for eating as the distance to the nearest cover increases (Lima et al. 1985). The squirrels in this study usually sat in the nut patch to eat nuts at the start of the session before they began caching bouts. If they were displaced by an aggressive conspecific, they moved just outside the patch or up into the branches of the tree nearest to the nut patch to eat. However, to check that out-of-view caching trips were not unusual, we carried out the analysis when the data were restricted to “in-view” caching trips as well as on all the data.

All visits to the nut patch were video recorded, and the films were used to score the number of squirrels in the nut patch whenever a focal squirrel collected a nut and the identities of any squirrels involved in aggressive interactions where one squirrel moved out of the nut patch when approached by another (displacements).

Search time rather than the original number of nuts was used as a variable in the analysis because, as more than one squirrel searched in the circle and took nuts from each patch, the number of nuts available when the focal squirrel was searching was not necessarily different in days that began with a different number of nuts. The time spent searching was also expected to be a more accurate indication of availability to the squirrels because they did not have visual access to all the nuts.

All statistical analyses were carried out using SPSS (v.14). The search time data were highly positively skewed and so were log transformed for analysis. The effect of the initial number of nuts on mean search time was analyzed with a repeated-measure ANOVA. The mode of the number of squirrels present at the different nut patches when each focal squirrel was searching and the mean numbers of displacements caused by each squirrel per session were analyzed with the nonparametric Friedman's test. Spearman's rank correlation (2 tailed) was used to test for correlations between travel time and the order of caches made within a day and between travel time and the day in which observations were made, separately for each squirrel. Multiple linear regression was used to produce a model of travel time with search time (common log transformed), observation site, social condition (the number of other squirrels present), and the interaction between search time and social condition as predictor variables. The variables making up the interaction term were transformed by centering them on the mean (search time) or 1 (social condition) (i.e., the mean or 1 was subtracted from each observation). Centering the data is the conventional approach when using regression to test interaction terms (Howell 2002, p 579). It has the effect of reducing the correlation between the individual variables and the interaction term and making the results of the regression analysis equivalent to those of an ANOVA using the same terms. All data collected from each squirrel were included in the analysis because variation between caches made by an individual may be considerable. This approach to analysis has been used in previous studies on caching birds (Petit et al. 1989; Brotons 2000). A dummy variable (Squirrel ID) was included as a predictor to take account of the variation due to individual squirrels.

RESULTS

Search time

There was no main effect of the number of nuts in the nut patch at the start of the session on the mean time squirrels spent searching for nuts ($F_{4,24} = 1.96$, $P = 0.13$), but there was a significant linear trend, with search time increasing as the number of nuts initially provided in the nut patch decreased ($F_{1,6} = 146.62$, $P < 0.0001$). There was no significant difference between sites ($F_{1,6} = 1.52$, $P = 0.26$) and no significant “site by number of nuts” interaction ($F_{4,24} = 0.91$, $P = 0.47$) (Figure 1).

Travel time model

Table 1 shows the coefficients for the variables included in the model. The model accounts for 34.7% of the variation found in travel time ($R^2 = 0.37$ or $R^2 = 0.35$, adjusted for the number of variables included in the model $F_{10,333} = 18.68$, $P < 0.0001$). Search time and the interaction between search time and social condition were significant predictors of travel time. For every 1 unit increase in log search time, squirrels took 193.78 s longer to return to the nut patch (unstandardized coefficient = 193.78 ± 17.77 , $t_{333} = 10.9$, $P < 0.0001$). This indicates that a 10-fold increase in search time adds 193.78 s to travel time and therefore that there is a greater effect on travel times when search times are short than when they are long. Figure 2 suggests that at short search times there was little difference between travel times in the presence or absence of another squirrel. As search time increased, increases in search time were associated with a smaller increase in travel time when conspecifics were present than when the squirrel was alone. In fact, in the presence of other squirrels the effect of search time was reduced by approximately 43% (unstandardized coefficient = -82.84 , $t_{333} = -3.48$, $P = 0.001$). Observation site and social condition alone had no significant effects on travel time. The inclusion of the dummy variable significantly improved the model, showing that there was a significant difference between individual squirrels' travel times (R^2 change = 0.028, F change_{6,323} = 2.413, $P = 0.027$).

The percentage of observations in which caches were made within view of the experimenter were BL 46.67%, NW 12.77%, PL 46.94%, RT 36.54%, SD 48.89%, MT 50%, HP 48.78%, and NK 44.68%. Squirrel NW was excluded from the analysis on “in view” caches, as only 6 of its caches were seen but all other squirrels made between 23 and 19 caches in view. Table 2 shows the coefficients for the variables included in the model when only observations of trips in which the experimenter saw the squirrel storing the nut were included in the analysis. The

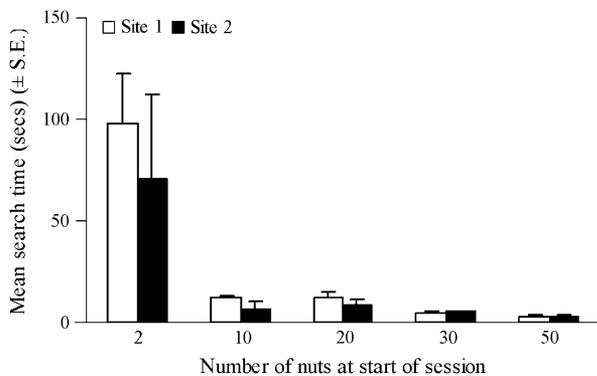


Figure 1 Mean search times (s) (± standard error [SE]) in each of the 5-nut conditions.

model accounted for 27.6% of the variation found in travel time ($R^2 = 0.33$, or $R^2 = 0.28$, adjusted for the number of variables included in the model $F_{10,134} = 6.09$, $P < 0.0001$). As in the overall model, search time (unstandardized coefficient = 219.44 ± 39.50 , $t_{134} = 5.56$, $P < 0.0001$) and the search time by social condition interaction (unstandardized coefficient = -127.14 ± 44.64 , $t_{134} = -2.85$, $P = 0.005$) were significant predictors of travel time. For every 1 unit of extra log search time, travel time increased by 65.72 s, and the presence of a conspecific reduced the effect by 57.9%. Observation site and social condition did not significantly affect travel time. The inclusion of the dummy variable did not significantly improve the model, showing that there were no significant differences between individual squirrels' travel times (R^2 change = 0.07, F change_{6,124} = 2.035, $P = 0.07$).

Observations on individual squirrels

Frequency of observations

All 8 of the identified squirrels were frequently present at the sites (Table 3).

When squirrels were searching for a nut, the number of other squirrels in the nut patch was 0, 1, or 2. This did not differ significantly according to the number of nuts initially provided in the patch ($\chi^2_4 = 1.48$, $N = 8$, $P = 0.83$). The exact number of other squirrels present across the site and visible to the experimenter was estimated from the amount of data collected per day from notes made during the observations; it did not exceed 5 and was more often only 1 or 2. There were no obvious differences in the number of squirrels seen between days with different densities of nuts in the nut patch.

Displacements

Squirrels were displaced from the nut patch by a conspecific on only 31 occasions. Squirrel RT at site 1 and NK at site 2 displaced the most squirrels, whereas PL at site 1 and MT at site 2 were displaced most frequently (Table 3). Squirrels tended to initiate more displacements at patches with a greater initial density of nuts, but the effect was not significant ($\chi^2_4 = 7.93$, $N = 8$, $P = 0.09$).

Travel times within and across days

None of the squirrels showed a significant correlation between travel time and the order in which caches were made within an experimental day, that is, travel time did not increase or

Table 1

Multiple linear regression coefficients for the time squirrels spent transporting nuts from and returning to the nut patch (travel time) according to the observation site, the time squirrels spent searching in the nut patch, and the social condition in which they searched

Variable	Unstandardized coefficient (±SE)	Standardized coefficient	<i>t</i>	<i>P</i>
Constant	220.55 (36.172)		6.1	<0.0001
Log search time	193.78 (17.77)	0.67	10.90	<0.0001
Observation site	-1.80 (22.65)	0.007	0.08	0.94
Social condition	36.33 (23.14)	0.17	1.58	0.12
Social condition × log search time	-82.84 (23.82)	-0.39	-3.48	0.001
Squirrel BL	41.70 (23.74)	0.10	1.78	0.08
Squirrel HP	-2.72 (22.65)	-0.07	-0.12	0.90
Squirrel MT	-19.12 (22.45)	-0.05	-0.85	0.40
Squirrel SD	-32.76 (21.95)	-0.09	1.49	0.14
Squirrel NW	36.67 (23.67)	0.09	1.53	0.13
Squirrel RT	-26.53 (22.47)	-0.07	-1.16	0.25

R^2 adjusted = 0.347, $F_{10,333} = 18.68$, $P < 0.0001$. SE, standard error.

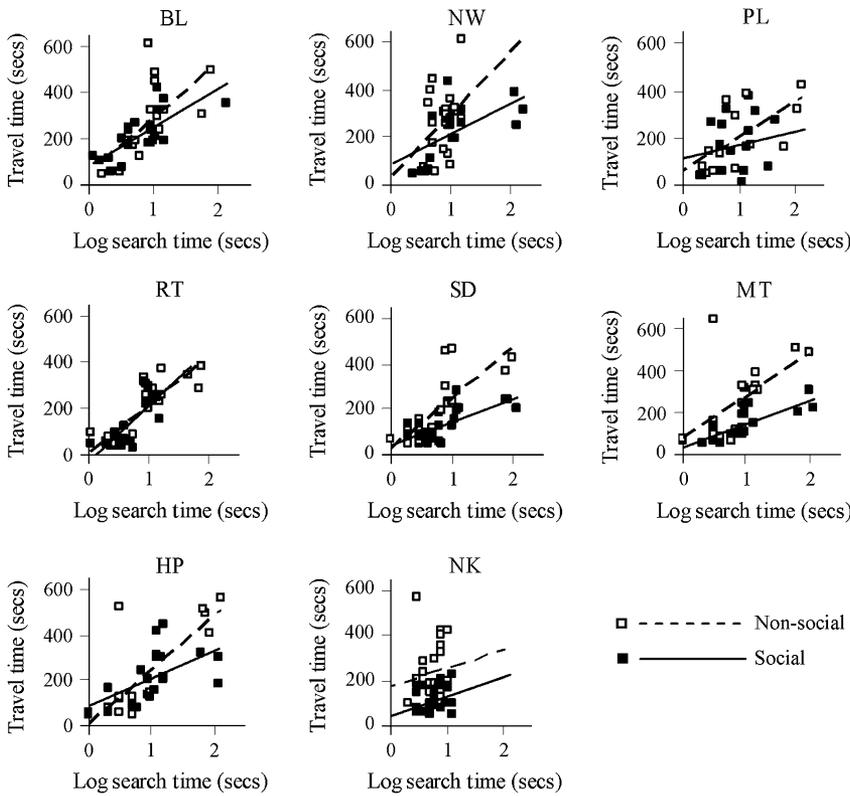


Figure 2
The multiple linear regression model fitted for squirrels at site 1 (BL, NW, PL, RT) and site 2 (SD, MT, HP, NK) when they were alone (nonsocial) or with one squirrel present (social).

decrease over the course of a day (HP, $r_s = -0.024$, $N = 40$, $P = 0.883$; NK, $r_s = -0.232$, $N = 45$, $P = 0.125$; PL, $r_s = -0.175$, $N = 44$, $P = 0.257$; RT, $r_s = -0.25$, $N = 44$, $P = 0.102$; SD, $r_s = -0.29$, $N = 44$, $P = 0.055$; BL, $r_s = 0.238$, $N = 38$, $P = 0.15$; MT, $r_s = 0.26$, $N = 41$, $P = 0.1$; NW, $r_s = 0.243$, $N = 38$, $P = 0.142$).

Five squirrels showed a significant negative correlation between travel time and the day in which observations were made with travel time becoming shorter on later days (BL, $r_s = -0.42$, $N = 38$, $P = 0.009$; NW, $r_s = -0.38$, $N = 41$, $P = 0.017$; MT, $r_s = -0.57$, $N = 41$, $P < 0.0001$; NK, $r_s = -0.46$, $N = 46$, $P = 0.001$; SD, $r_s = -0.37$, $N = 44$, $P = 0.013$). The other 3 squirrels showed no significant correlation (RT, $r_s = -0.15$, $N = 44$, $P = 0.336$; PL, $r_s = 0.11$, $N = 44$, $P = 0.488$; HP, $r_s = 0.29$, $N = 40$, $P = 0.07$). A single χ^2 value was obtained

from the individual P values using the χ^2 transformation described by Jones and Fiske (1953). (The $P < 0.0001$ for squirrel MT was taken as $P = 0.0001$; for positive correlations, $1 - P$ was used.) ($\chi^2_{16} = 62.16$, $P < 0.0001$). The null hypothesis that none of the squirrels showed a trend for travel time to reduce over days can be rejected.

DISCUSSION

The squirrels in this study appeared to adjust their food sequestering activities in relation to both the availability of food and

Table 2
Multiple linear regression coefficients for the model of travel time when only data from observations in which squirrels made a cache in view of the experimenter were included

Variable	Unstandardized coefficient (\pm SE)	Standardized coefficient	t	P
Constant	89.09 (214.85)		0.42	0.68
Log search time	219.44 (39.50)	0.74	5.56	<0.0001
Observation site	52.99 (109.04)	0.206	0.486	0.63
Social condition	65.72 (38.03)	0.28	1.73	0.09
Social condition \times log search time	-127.14 (44.64)	-0.56	-2.85	0.005
Squirrel BL	143.02 (110.16)	0.37	1.30	0.20
Squirrel HP	70.10 (34.13)	0.2	2.05	0.04
Squirrel MT	43.78 (33.33)	0.13	1.31	0.19
Squirrel SD	-9.18 (32.77)	-0.03	-0.28	0.78
Squirrel PL	94.77 (109.41)	0.26	0.87	0.39
Squirrel RT	70.49 (110.26)	0.18	0.64	0.52

R^2 adjusted = 0.276, $F_{10,134} = 6.09$, $P < 0.0001$. SE, standard error.

Table 3
The number of days each squirrel was present at the observation site and the number of times each squirrel displaced other squirrels from the nut patch

Site 1		Number of displacements by focal squirrel				
Focal squirrel	Days	RT	PL	BL	NW	Unidentified
RT	30	—	4	3	2	3
PL	24	0	—	0	0	0
BL	23	0	3	—	0	1
NW	19	0	0	0	—	0
Site 2		Number of displacements by focal squirrel				
Focal squirrel	Days	HP	SD	NK	MT ^a	Unidentified
HP	23	—	0	0	0	0
SD	21	0	—	0	3	0
NK	20	4	2	—	2	1
MT	16	0	0	0	—	0

^a MT was also displaced by unidentified squirrel(s) on 2 occasions.

to the level of competition at the food source. To our knowledge, this is the first study to show that, when collecting and caching food from a central source, a scatter-hoarding mammal responds to conspecifics at the food source primarily as competitors for the food rather than as potential pilferers.

When food is abundant, the presence of conspecifics does not greatly affect the availability of food, but when food is limited and there is competition for it, hoarders must sequester it more rapidly in order to maximize the amount they secure. In the current study, the social condition by search time interaction was a significant predictor of travel time, showing that squirrels did indeed return to the nut patch relatively more rapidly as competition increased. Heinrich and Pepper (1998) found that captive ravens also cached more quickly when conspecifics were present than when they were alone when a relatively small quantity of meat was provided (15 chunks between 4 birds) but that wild ravens storing food from a carcass cached more rapidly when they were with one other bird (their mate) than when a large flock was present. This is in contrast to the current study, in which social condition had no main effect on the squirrels' travel time and little influence at all when food was abundant. This could indicate a difference between the species, with ravens responding to conspecifics as potential pilferers and squirrels as competitors for the food. Ravens have been found to steal caches they have seen being made and caching at greater distances from where others are foraging may help to prevent this (Heinrich and Pepper 1998; Bugnyar and Kotrschal 2002). These birds can also be aggressive around the food source, sometimes preventing others from accessing it (Heinrich and Pepper 1998), so spending longer on making caches may also partly be a result of avoiding such aggressive encounters. It is not known whether squirrels can use observational spatial memory to steal from caches they see others making, but the squirrels in the current study showed little aggression, only occasionally chasing each other off the nut patch and no squirrels were completely excluded from it. For squirrels, responding to conspecific competitors by increasing the rate at which they exploit the nut patch should be more beneficial than increasing the time spent on cache protection measures.

Responding to conspecifics flexibly according to the availability of food rather than directly to their presence should allow the squirrels to maximize the amount they store that survives for later use over a range of different conditions. Previous studies in which animals were provisioned with an abundant supply of food found a reduction in the rate of caching in response to the presence of conspecifics (Stone and Baker 1989; Lahti and Rytönen 1996; Brotons 2000; Dally et al. 2005), and in our own previous work we found that squirrels traveled farther between bouts of digging (Leaver et al. 2007) and spent more time arranging leaf litter over the surface of the cache (Hopewell and Leaver forthcoming) when conspecifics were present than when they were alone. Together with the result of the current study, this supports the idea that eastern gray squirrels respond differently to the presence of conspecifics according to whether they are competing at the food source or forming an "audience" to the caching event, where they represent potential pilferers.

The overall model suggests that there were significant differences between travel times of individual squirrels. There were very few physical interactions, so it is unlikely that any squirrels were particularly excluded from the nut patches, although 2 squirrels, one at each site, instigated most of the displacements and so were indicated as the most dominant individuals (squirrels RT and NK). Squirrel NK was pregnant when she was first trapped and dyed, so it is likely that she was nursing young during the study, and this may have made her more aggressive. Interestingly, these 2 squirrels appeared to be least affected

by changes in competition for the food but in different ways. Squirrel RT showed very little difference between the social and nonsocial conditions across the different search times, whereas NK tended to return to the nut patch sooner in the social than nonsocial condition. It is possible that this difference relates to the location of their home ranges. All 8 squirrels were seen at the sites very frequently, which suggests that the nut patches were placed well within their normal foraging range, but as previous studies suggest that squirrels transport food toward the center of their home ranges where it can be stored more securely (Kraus 1983; Spritzer and Brazeau 2003), the exact position of the nut patches may have affected travel times. The lack of a significant difference between squirrels when the analysis was restricted to observations of trips in which caches were made in view of the experimenter, and therefore within a restricted distance of the nut patch, supports the idea that home range location was influential on travel time, although some caution is needed in the interpretation of this result due to the reduced power of the test caused by excluding data. There was no indication that the number of displacements initiated by individual squirrels was related to the likelihood that they would remain close to the nut patch to make caches, as the most dominant squirrels made no more caches in view of the experimenter than most of the other squirrels. These points suggest that it is the amount of competition rather than the type of competition that influences travel time. The influence of home range location and dominance on how competition is perceived may differ between individual squirrels, and this could explain why one squirrel (NW) went out of view very frequently, but further study is needed to assess the importance of these factors on travel time.

The lack of a significant main effect of conspecific presence on travel time shows that squirrels did not respond directly to conspecifics by increasing transport distance. The pattern of travel times within and between sessions also suggests that squirrels were not trying to minimize pilferage risk in response to the social factors during individual sessions. Squirrels showed no tendency to carry nuts increasingly far away over the course of a session, as predicted by optimal density models (Stapanian and Smith 1978; Clarkson et al. 1986), and 5 of the squirrels returned to the nut patch increasingly quickly from one session to the next. This is the opposite of what is expected of hoarders aiming to maximize cache survival when hoarding from a recurring food source (Waite and Reeve 1992b). It is possible that these squirrels learned that the nut patch was available for a certain period of time each day and so deliberately shortened their travel times to maximize the number of nuts they sequestered during that time. The squirrels may also have moved their stored food to more secure locations at a later time, as has been found in other scatter hoarders (Merriam's kangaroo rats, Jenkins and Peters 1992; gray jays, Waite and Reeve 1992a; willow tits, Brodin 1994; scrub jays, Emery and Clayton 2001). Although the squirrels were not seen to do this, it may have occurred over the longer term. The fact that travel times did not increase between sessions suggests that the ground around the nut patches did not become saturated despite the frequent provisioning of nuts during the study.

The presence of conspecifics alone did not affect travel time but travel time was affected by the availability of nuts independently of social condition and squirrels appeared to respond to reduced availability by caching in more distant locations. As expected, the time squirrels spent searching for nuts increased as the number of nuts provided decreased and the model indicates that as the time squirrels spent searching increased they took longer to transport the nuts and return to the patch. This suggests that, although the squirrels did not respond to social

factors by increasing the distance between their caches and the nut patch, they did respond to a reduction in food availability by trying to minimize pilferage risk. Storing food farther from the source increases a cache's chances of survival (e.g., Tamura et al. 1999), and previous studies have also found that scatter hoarders distribute food more widely if it is rare in the environment (willow tits and crested tits, *Parus cristatus*, Jokinen and Suhonen 1995; heteromyid rodents, Longland and Clements 1995).

Previous studies have found that scatter hoarders respond flexibly to local conditions, adjusting the time they spend transporting and collecting food according to variations in background pilferage risk (magpies, Clarkson et al. 1986), the presence of existing caches (gray jays, Waite and Reeve 1992b; coal tits, Male and Smulders 2007b) and the nutritional value of the food being stored (willow and crested tits, Jokinen and Suhonen 1995; Merriam's kangaroo rats, Leaver 2004). The current study extends this finding to include their response to conspecifics at the food source and suggests that, in contrast to larder-hoarding animals (eastern chipmunks, Clarke and Kramer 1994), scatter hoarders respond to conspecifics primarily as competitors at the food source rather than as potential pilferers. Further work is needed to establish to what extent competition for food rather than pilferage risk determines the compromise made between collecting and transporting food for long-term caches versus short-term caches which are to be redistributed.

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