

Natural History Note

Eavesdropping Squirrels Reduce Their Future Value of Food under the Perceived Presence of Cache Robbers

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ABSTRACT: Caching behavior frequently occurs within a social context that may include heterospecific cache pilferers. All else equal, the value of cacheable food should decline as the probability of cache recovering declines. We manipulated gray squirrels' (*Sciurus carolinensis*) estimate of the probability of cache recovery using experimental playbacks of the vocalizations of a potential cache robber, the blue jay (*Cyanocitta cristata*). We used giving-up densities (GUDs) to quantify relative changes in squirrels' valuation of cacheable and noncacheable foods. We collected GUDs during playback experiments to test whether squirrels (1) eavesdrop on vocalizations to detect jay presence, (2) devalue cacheable food in the (perceived) presence of jays (i.e., perceive jays as cache pilferers), and (3) are sensitive to distant effects (i.e., lower devaluation of cacheable food at sites far from the perceived location of jays). Consistent with our predictions, squirrels decreased the value of cacheable hazelnuts by two nuts, on average, during jay playbacks, but only at foraging stations near the jay playback sites. We conclude that through eavesdropping, squirrels assess site-specific risks of cache pilfering and alter their caching behavior to reduce the likelihood of pilferage. Evidence suggests that tree seed consumers in eastern deciduous forests exist within a complex communication network.

Keywords: *Cyanocitta cristata*, eavesdropping, food caching, future value, giving-up density, *Sciurus carolinensis*.

The explicit recognition that much of animal communication occurs within a communication network (several animals within signaling and receiving range of one an-

other; McGregor 2005) represents a paradigm shift away from dyadic (one signaler–one receiver) interactions. Importantly, the network paradigm recognizes the role of eavesdroppers and audiences (i.e., third-party individuals) on the evolution and ecology of communication systems and social interactions that may depend on communication for their maintenance (e.g., indirect reciprocity; Nowak and Sigmund 1998). Eavesdroppers acquire information from the communication between two or more other individuals. In the case of interceptive eavesdropping (Wiley 1983; Peake 2005), the information acquired pertains to some aspect of the environment (e.g., predation risk; Randler 2006; Templeton and Greene 2007; K. A. Schmidt, E. Lee, R. S. Ostfeld, and K. E. Sieving, unpublished manuscript). If assessing information in this fashion confers an advantage to the eavesdropper, then eavesdropping behavior is expected to evolve (McGregor 1993; Peake 2005). In turn, the communicating individual(s) may further facilitate or impede the flow of information, depending on whether an informed eavesdropper has positive or negative fitness consequences for the communicator (e.g., Deecke et al. 2005). While interceptive eavesdropping has frequently been examined in predator-prey interactions (Cade 1975; Ryan et al. 1981; Zuk and Kolluru 1998; K. A. Schmidt, E. Lee, R. S. Ostfeld, and K. E. Sieving, unpublished manuscript), eavesdropping by individuals vulnerable to kleptoparasitism (i.e., pilferage of cached food) has not, to our knowledge, been explicitly examined.

Food caching has independently evolved numerous times in diverse taxa (Vander Wall 1990), some of which are social, for example, Paridae (titmice and chickadees), Corvidae (crows, jays, and magpies), and Sciuridae (squirrels, chipmunks, and marmots). However, even among asocial species, caching behavior frequently occurs within a social context that may include heterospecifics (Bednekoff and Balda 1996; Emery and Clayton 2001; Dally et al. 2006a, 2006b; Leaver et al. 2007). Thus, from the perspective of a cacher (defined here as an individual who caches food), the world is often replete with potential cache robbers (or pilferers) who may learn the location of caches

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by observing the cacher's behavior. With the possible exception of kin or mates (Goodwin 1956; Dally et al. 2006a), informed pilferers represent a fitness cost to the caching individual through pilfered caches. To prevent such losses, cachers possess diverse behaviors that reduce pilferage (Vander Wall 1990; Dally et al. 2006a).

Consider eavesdropping within the food cacher–pilferer system. Cachers should attempt to collect information on the presence and location of pilferers, who in turn may attempt to conceal themselves. When pilferers are present (or are perceived to be present), cachers should reduce or degrade the information available to pilferers regarding cache locations or otherwise alter their caching behavior. While multiple pilferage-reducing behaviors exist (Vander Wall 1990; Dally et al. 2006a), many of them probably collapse into a single ultimate explanation: a decrease in the probability of cache recovery (i.e., an increase in the probability that a cache will be pilfered) reduces the future value of food. As a result, in the presence of pilferers, food should be cached (1) less often or not at all (Stone and Baker 1989; Carrascal and Moreno 1993) or (2) in locations that reduce the quantity or quality of information available to pilferers, for example, at greater distance from the pilferer or in less apparent locations (Dally et al. 2005). The latter would be likely to incur a greater cost to caching behavior but would simultaneously increase the future value of food through reducing the probability of theft.

Here we examine cacher–pilferer interactions in the well-known temperate forest system that consists of gray squirrels (*Sciurus carolinensis*) and blue jays (*Cyanocitta cristata*). Both species routinely cache food (e.g., acorns), particularly in advance of winter food shortage (Darley-Hill and Johnson 1981; Jacobs 1989; Vander Wall 1990; van der Merwe 2004). Jays and other corvids use observational spatial memory to re-locate caches (Clayton et al. 2001; Bednekoff and Kotrschal 2002). Therefore, jays observing squirrels as they cache food represent a real threat to cache recovery. In our study, we examined the influence of the perceived presence of jays on squirrel caching behavior: squirrels are cachers and jays are pilferers in our system. We used the technique of giving-up densities (GUDs) to quantify relative changes in squirrels' valuation of cacheable (having current and future value) and non-cacheable (having current value only) foods: hazelnuts with and without their shells, respectively. We collected GUDs during experimental playback of jay vocalizations to test whether squirrels (1) eavesdrop on blue jay vocalizations to detect jay presence, (2) devalue the future value of food in the (perceived) presence of jays (i.e., perceive jays as cache pilferers), and (3) are sensitive to distant effects, reducing future value less at sites far from the perceived location of jays.

Methods

Study Site

We studied free-living gray squirrels on the property of the Institute of Ecosystem Studies (IES), located in Dutchess County in southeastern New York. IES contains approximately 325 ha of eastern deciduous forest, dominated by oaks (*Quercus rubra* and *Quercus prinus*) and sugar maple (*Acer saccharum*), mixed with grassy meadows and old-field habitats. We conducted our studies at two sites at forest/meadow boundaries (Field Lab and Plant Science Building) separated by >2 km, each of which has an abundant gray squirrel population. Blue jays are fairly common at IES but have large winter home ranges and thus are not readily seen or heard on any given day in a walk through IES property (K. A. Schmidt, personal observation). On occasion, red squirrels were also seen at two of the four stations at the Field Lab site, but their smaller stature makes them inefficient foragers on nuts buried in pea gravel (see next paragraph), and they are unlikely to have contributed to the results shown here.

Giving-Up Densities

We used the technique of giving-up densities from artificial food patches to quantify changes in the marginal rate of substitution (MRS) of cacheable for noncacheable food, following the technique used by Schmidt et al. (1998) and Schmidt (2000). An individual foraging in an artificial food patch experiences diminishing returns as its harvest rate declines with time spent in the patch. Under diminishing returns, an animal should exploit a patch until its harvest rate (H) declines to the sum of its foraging costs, which include metabolic (C), predation (P), and missed-opportunity costs (MOC); that is, the point at which $H = C + P + \text{MOC}$ (Brown 1988). The density of remaining food at which this relationship is satisfied and the forager ceases exploiting the patch is its giving-up density, or GUD (Brown 1988, 1992). The MRS of two food patches is simply the ratio of their marginal values (Schmidt et al. 1998), where the marginal value of a food patch in turn is equivalent to the patch quitting-harvest rate, that is, the amount of energy obtained per unit time spent in a patch at the point where the forager ceased exploiting the patch. Thus, the ratio of quitting-harvest rates from two separate patches exploited by the same forager indicates the exchange rate of time spent in one patch for time spent in the second patch. For changes in the value of one food type (say, cacheable food) to be detectable, its value must be quantified simultaneously with that of another food type (noncacheable) across treatments that are predicted to change one or the other value. An analysis, such as ANCOVA (Schmidt et al. 1998; Schmidt 2000), is used to

quantify the value of one food while statistically holding the value of the paired food constant.

We collected GUDs from artificial food patches following the design used by van der Merwe (2004), who quantified the value of cacheable and noncacheable foods in fox squirrels (*Sciurus niger*). Patches consisted of a plastic tray (30 cm × 20 cm × 40 cm) filled with 20 L of pea gravel (mostly measuring 3–8 mm in diameter but with a small amount of coarser material) into which we thoroughly mixed 15 hazelnuts. Van der Merwe (2004) used 14 nuts per tray and failed to significantly increase GUDs when an additional 28 nuts were provided ad lib., and they concluded that satiation effects were not operating. Given the number of nuts used in our experiments, this result appears robust to our study. Furthermore, we follow Kotler et al. (1999) and van der Merwe et al. (2007) in considering hazelnuts with their shells intact as cacheable and nuts with shells removed as noncacheable. Kotler et al. (1999) noted that hazelnuts with their shells intact are rarely consumed (1 of 55 nuts presented to fox squirrels), whereas hazelnuts with shells removed are rarely cached (3 of 55 nuts). Occasionally squirrels did remove shells from hazelnuts and consumed them at the tray, as noted by the presence of shell fragments. However, these observations were uncommon, and only a fraction of the nuts removed were consumed at the tray. Furthermore, these hypotheses are conservative in regard to our classification of cacheability; that is, changes in the relative value of the two types of food require that the two foods are qualitatively unique (have future value or not).

Vocalizations and Playbacks

We recorded unique blue jay vocalizations onto CDs for use in the experimental playbacks. We made three unique jay CD types (to prevent pseudoreplication; see Kroodsmas 1989) based on recordings of blue jays commercially available as well as recordings made by K. A. Schmidt in Lubbock, Texas, and Millbrook, New York. Each CD contained unique calls from three different call groups (following Tarvin and Woolfenden 1999): (1) jeer group, including the “jay” calls, (2) pumphandle group, including the “squeaky gate” call, and (3) intrapair contact calls, including “kuk” or “kuet” calls. Each CD contained representations of each group and call type arranged as a sequence of call tracks interspersed with silent tracks ranging from 30 s to 7 min. In total, each CD contained 38–42 min of silent tracks and 17–19 min (29%–32%) of call tracks. We used a single control CD that consisted of songs and calls of multiple passerines common at IES in the winter: northern cardinal (*Cardinalis cardinalis*), eastern bluebird (*Sialia sialis*), American goldfinch (*Carduelis tristis*), and dark-eyed junco (*Junco hyemalis*). These species

are largely granivorous in the winter but do not consume larger nuts, such as acorns (or hazelnuts). Each species was recorded on a separate track rather than all together as a chorus, and like the jay tracks, passerine tracks (30% of the total playback time) were interspersed with silent tracks. During playback, the CD player was set to “repeat all”; tracks played in the order in which they were recorded, and the whole sequence was repeated until the CD player was turned off.

Experimental Setup

Our experiment began after an initial prebaiting period to ensure squirrel activity and familiarity with foraging in the trays. During the experiment, trays were open between 0800 and 1600 hours. To broadcast the vocalizations during the experiment, we attached a CD player to one Saul Mineroff amplified speaker (model SME-AFS) placed ~2 m high in a tree. Maximum sound intensity of jay and control playbacks was measured as 90 db at 1 m using a sound pressure meter. Three CD player–speaker units were used per site, each playing the same CD type. We randomized jay and control playbacks per site, following the schedule in table 1. Right and left designations in the table refer to opposite ends of the long axis of the station layout at each site (fig. 1). The CD player–speaker units were placed at only one end to test for an effect of distance on squirrels’ responses. Squirrels could forage either in near sites (~25 m from the source of calls) or in away sites (~125 m from the nearest source). Trees were bare during winter, when this study was conducted, and sound transmission was efficient such that blue jay vocalizations were audible but not easily heard under background noise to a human listener across this distance. Each station contained two trays, one containing 15 hazelnuts in their shells (cacheable food) and the second containing hazelnuts with shells removed (noncacheable food), with the relative position of the foods (i.e., left or right tray) randomized between days and stations. At the termination of each daily trial, the playback equipment was turned off and taken

Table 1: Sequence of playback presentations at each study site over an 8-day trial

| Day | Plant Science | |
|-----|---------------|-----------|
| | Building | Field Lab |
| 1 | Jay left | Control |
| 2 | Control | Jay left |
| 3 | Jay right | Control |
| 4 | Jay left | Control |
| 5 | Control | Jay right |
| 6 | Control | Jay left |
| 7 | Jay right | Control |
| 8 | Control | Jay right |

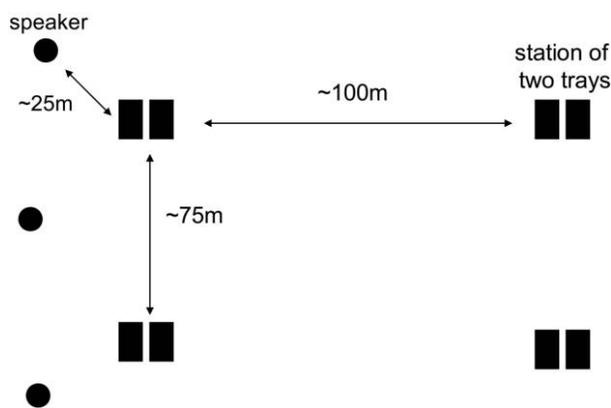


Figure 1: Schematic representation of the experimental design showing the placement of speakers used for playbacks.

down, and the remaining uneaten hazelnuts were removed from the trays by spreading out the gravel and carefully searching for nuts. GUDs were quantified as the number of uneaten nuts remaining in a tray. We collected 14 days of data between December 28, 2006, and January 29, 2007, following the schedule in table 1 (day 9 of data collection restarted the sequence at day 1). For analyses, we discarded data from a station if the GUD of either tray exceeded 12 (i.e., at least three hazelnuts must be removed from each tray; only 13 of 112 station days were discarded). Data were analyzed using SYSTAT, version 10. Statistical significance was set at $\alpha = 0.05$.

Results

Comparison of the Jay Playbacks

To test whether GUDs or cacheability (hazelnuts with and without shells) were differently affected by the three types of jay playbacks (i.e., the three unique sets of vocalizations played to squirrels), we used ANOVA with GUD as the dependent variable and site, playback, food (hazelnuts with or without shells), and the interaction between playback and food as the independent variables. Site ($F = 7.23$, $df = 1, 91$, $P = .009$) and food ($F = 16.03$, $df = 1, 91$, $P < .001$) were the only significant effects ($r^2 = 0.256$). Neither the type of playback ($F = 1.20$, $df = 2, 91$, $P > .30$) nor the interaction term with food ($F < 0.10$, $df = 2, 91$, $P > .50$) significantly affected GUDs. Based on these results, for the remainder of the analyses we considered data collected under any of the three jay playbacks as “jay near” treatment for stations near (25 m) the playbacks and “jay away” for stations at a distance (125 m) from the playbacks. After we confirmed that there was no distance effect with the control playbacks ($F < 0.50$, $df = 1, 93$,

$P > .90$), stations both near and away from the playback were pooled to make up the control treatment.

Cacheable versus Noncacheable

To test whether playback treatments and cacheability affected GUDs, we used a partially hierarchical ANOVA ($r^2 = 0.756$) with GUD as the dependent variable and day, site, station (nested within site), treatment ($n = 3$; jay near, jay away, control), food, and the interaction between treatment and food as the independent variables. All main effects were significant (table 2). Cacheable hazelnuts in the shell had significantly higher GUDs than noncacheable nuts without the shell (cacheable GUD = 5.74 ± 0.35 , noncacheable GUD = 3.40 ± 0.37). Fewer hazelnuts were consumed during the jay near treatment than during either the control ($P < .001$; Tukey HSD) or the jay away ($P = .016$; Tukey HSD) treatment (fig. 2). Finally, the significant interaction between treatment and food (table 2; fig. 2) was driven by a larger increase in the GUD of cacheable nuts for the jay near treatment, suggesting a change in the MRS of foods. This was further confirmed using a similarly constructed ANOVA separately on each food type. Treatments (jay near, jay away, control) had a significant effect on cacheable nuts only (cacheable: $F = 11.6$, $df = 2, 76$, $P < .001$; noncacheable: $F = 0.40$, $df = 2, 76$, $P > .70$).

Changing Future Value

To more clearly isolate the effect of playbacks on squirrels' future value of food, we used an ANCOVA with cacheable GUD as the dependent variable, noncacheable GUD as the covariate, and site, station (nested within site), and treatment (jay near, jay away, control) as main effects. We initially tested for an effect of the interaction between covariate and treatment. The interaction was nonsignificant ($F = 0.762$, $df = 2, 73$, $P > .45$), so we assumed homogeneity of slopes and subsequently dropped the interaction term from the final model. The covariate, site, station, and treatment effects were all significant (table 3). For any fixed GUD on noncacheable food, squirrels low-

Table 2: ANOVA ($r^2 = 0.256$) testing for the effects of differences in giving-up densities among days, treatments, sites, and patches

| Effect | df | MS | F | P |
|------------------------|-----|-------|-------|-------|
| Day | 13 | 13.68 | 3.472 | <.001 |
| Site | 1 | 488.1 | 123.9 | <.001 |
| Station(site) | 6 | 182.1 | 46.24 | <.001 |
| Playback | 2 | 31.88 | 8.095 | <.001 |
| Food | 1 | 292.8 | 74.36 | <.001 |
| Playback \times food | 16 | 18.12 | 4.601 | .011 |
| Error | 175 | 3.938 | | |

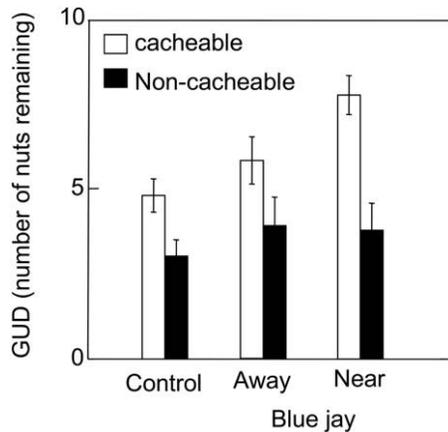


Figure 2: Mean giving-up density (GUD; number of remaining hazelnuts \pm SE) as a function of food type and playback treatments.

ered their value of cacheable food by the equivalent of two hazelnuts, on average, in the jay near treatment in comparison to both the control ($P < .001$; Tukey HSD) and jay away treatments ($P = .002$; Tukey HSD). The latter two did not differ from each other ($P > .90$; Tukey HSD; fig. 3).

Discussion

Animals assign future value to food that can be stored and consumed at a later date (Gendron and Reichman 1995; Kotler et al. 1999). In the closely related fox squirrel, Kotler et al. (1999), van der Merwe (2004), and van der Merwe et al. (2007) have demonstrated how the future value of food (also using hazelnuts with intact shells) varies as a function of the availability of both noncacheable (current value) and cacheable (future value) food. We have extended these analyses to examine how future value is also a function of the likelihood of retrieving caches. All else equal, the value of cacheable food should decline as the probability of its recovery declines. In our experiment, we manipulated squirrels' estimate of the probability of cache recovery by playing vocalizations of a common potential cache robber, the blue jay (Steele and Koprowski 2001). We predicted that if squirrels equated the presence of jays with lower cache recovery, squirrels would reduce the value of cacheable food. Consistent with our predictions, squirrels decreased the value of patches containing cacheable hazelnuts by two nuts, on average, during jay playbacks. The only other study we know of that has attempted to manipulate the perceived presence of potential cache robbers through vocalizations alone is Gammon and Baker's (2004) study with black-capped chickadees (*Poecile atricapillus*). They found that chickadees in the laboratory did

not alter caching behavior (latency to first cache, number of items cached) when played vocalizations of conspecifics. It is possible that these behaviors or the laboratory setting that offered seeds freely in a dish, as opposed to making the animal work to obtain resources, are not ideal test conditions or, alternatively, that chickadees did not associate the calls with the possibility of cache pilfering.

The effects we demonstrated were seen only for stations near the jay playback sites. Results from stations more than 100 m away from playbacks were almost identical to those from the control treatment. This distance effect is understandable, given the nature of cache recovery in corvids. Corvids rely on observational spatial memory for retrieving caches, and the efficacy of observational spatial memory should decrease with distance between cacher and pilferer (Burnell and Tomback 1985; Clayton et al. 2001; Bednekoff and Kotschal 2002).

Given the nature of our experiment, we do not have direct evidence that blue jays stole caches of gray squirrels. However, observations by other researchers demonstrate that cache pilfering does occur, particularly if jays see an individual make a cache. Blue jays are known to steal caches of gray squirrels, often soon after a seed is cached (Steele and Koprowski 2001). Likewise, Thayer and Vander Wall (2005) used aviary experiments to show that the congener Steller's jay (*Cyanocitta stelleri*) is capable of finding seed caches of yellow pine chipmunks (*Tamias amoenus*). Steller's jays also steal the caches of heterospecific jays when they observe them caching food (Burnell and Tomback 1985).

Alternative explanations for our result that the relative value of cacheable food declines in the perceived presence of jays include (1) squirrels increased the absolute value of noncacheable food (rather than decreasing the absolute value of cacheable food) and (2) only when foraging on cacheable food did squirrels increase their missed opportunity cost and, in turn, increase GUDs, because of com-

Table 3: ANCOVA ($r^2 = 0.686$) testing for the effects of treatment (jay vocalizations) on the relative value of cacheable food

| Effect | df | MS | F | P |
|----------------------------------|----|-------|-------|-------|
| Giving-up density (noncacheable) | 1 | 30.40 | 7.253 | .008 |
| Site | 1 | 100.3 | 23.94 | <.001 |
| Station(site) | 6 | 13.00 | 3.101 | .008 |
| Treatment ^a | 2 | 40.35 | 9.627 | <.001 |
| Jay away vs. control | | | | .987 |
| Jay near vs. jay away | | | | .002 |
| Jay near vs. control | | | | <.001 |
| Error | 88 | 4.191 | | |

^a Under "treatment," we show the results of all pairwise comparisons (Tukey HSD).

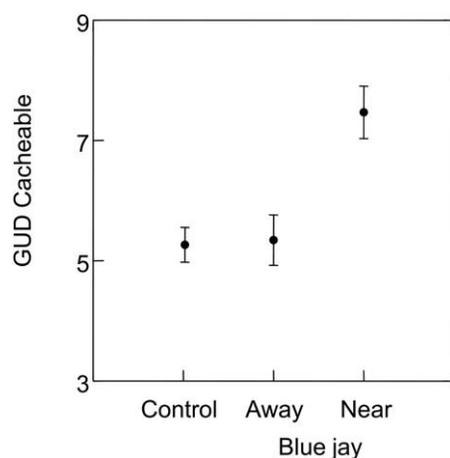


Figure 3: Mean giving-up density (GUD) on cacheable food (number of remaining hazelnuts in the shell \pm SE) for a fixed GUD on noncacheable food across the three playback treatments.

petition with jays for noncacheable food. The first explanation can be ruled out by the absence of changes in GUDs on noncacheable food (fig. 2); instead, the change in relative value is driven solely by changes in GUDs on cacheable food. The second alternative also seems unlikely. Jays are not capable of foraging in the trays, aside from taking an occasional nut off the surface, and with trays next to each other, squirrels can defend trays from jays.

Noncacheable food had greater value than cacheable food in our experiment. This contrasts with the two other studies that have measured the relative future value of hazelnuts. Kotler et al. (1999) and van der Merwe (2004) used different methods to arrive at similar estimates of relative future value: cacheable hazelnuts with intact shells had 44% (Kotler et al. 1999) and 37% (van der Merwe 2004) higher value than hazelnuts with shells removed. Why cacheable hazelnuts were less valuable than noncacheable nuts in our study is not known but may be related to the large acorn (*Quercus* spp.) masting event at the site during the autumn of 2006, which provided a ready source of cacheable seeds up to a few months before our experiment commenced.

Eavesdropping and the Implicit Eavesdropper Hypothesis

The perceived presence of jays, through the use of experimental playbacks, was sufficient to elicit a change in the future value of food by squirrels. Hence, in the absence of any additional information on the motivational state or behavior of jays, the behavior of squirrels is consistent with the assumption that squirrels implicitly treated jays as pilferers; jays are guilty before proven innocent. We refer to this phenomenon as the implicit eavesdropper hypoth-

esis. That is, squirrels equate the presence of jays (i.e., vocalizations) with the loss of caches, which implies that jays observe (eavesdrop on) squirrels as squirrels cache food. We arrived at this conclusion through the changes in squirrel behavior revealed through GUDs rather than a direct test of the hypothesis. Other studies have shown that cache protection behavior is dependent on the motivation of the potential pilferer. For instance, caching rooks (*Corvus frugilegus*) are not secretive when nearby conspecifics are also engaged in caching behavior (Källänder 1978). In contrast, Leaver et al. (2007) demonstrated that gray squirrels used cache protection behaviors (greater cache spacing, orientation of poster to conceal activity when caching) when their audience consisted of conspecifics but not when it consisted of heterospecifics (carrion crow *Corvus corone* or magpie *Pica pica*). Additional studies are necessary to determine whether there are any generalities one can make regarding the use of additional information on motivation. Since jay presence was staged in our experiment, whether squirrels would attempt to collect additional motivational information could not be determined. Nonetheless, in the absence of such information, we can conclude that squirrels apparently treat jays as pilferers, although we cannot entirely exclude the absence of additional information that would have been provided by real jays in our experiment. Given that the playback experiments were run in the absence of an observer, it is possible, although unlikely, that jays aggregated near the speakers during playbacks. However, jays were not apparent during casual observations of stations during the day (R. S. Ostfeld, personal observation). Likewise, during jay playbacks in other contexts, birds that do respond to calls of conspecifics typically disperse shortly afterward (K. A. Schmidt, personal observation).

Conclusions

Our results suggest that squirrels (1) use jay vocalizations as cues to the presence of jays, (2) use jay vocalizations to approximate the distance between themselves and jays and hence the risk of cache pilferage, and (3) implicitly perceive jays as pilferers in the absence of additional (e.g., visual) information. We hypothesize that in addition to devaluating the value of cacheable food in the presence of jays, squirrels should employ strategies to decrease the likelihood of pilferage and reduce information flow to jays, such as those reported by Leaver et al. (2007). If jays benefit by robbing squirrels' caches, they should also reduce their likelihood of being detected through vocalizing. Thus, squirrels may be a selective force on jay communication under certain contexts. These last two conjectures remain untested, but they are consistent with the suggestion that cache and pilfer strategies exist as an evolutionary game of interspecific klep-

toparasitism (Vander Wall and Jenkins 2003; Dally et al. 2006a), which may have repercussions for the evolution of communication and eavesdropping within and between species. In terms of attempts to detect or curtail the transmission of information, interspecific kleptoparasitism may superficially resemble the game between predator and prey (Brown et al. 1999). As such, we might expect cachers to set a baseline level of suspicion of being watched (analogous to apprehension in predator-prey games; Kotler et al. 2004) that is unlikely to ever reach zero, even in the absence of pilferers (see Brown et al. 1999). Thereby pilferers may exert important but subtle behavioral effects in cachers beyond the more obvious loss of caches.

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Gray squirrel (*Sciurus carolinensis*). Photograph by Sylvia L. Halkin.