SOCIAL HOARDING AND A LOAD SIZE–DISTANCE
RELATIONSHIP IN GRAY JAYS[1]

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A model that assumes scatterhoarders maximize the rate at which they store food that survives density-dependent theft by competitors has been developed elsewhere (Waite 1991a; Waite and Reeve 1992a, 1992b). The model addresses the questions of how such hoarders should distribute caches of food items collected from an ephemeral, locally abundant source, and how long they should persist in caching from such a source before moving on in search of alternative sources. The results of several field experiments using Gray Jays (*Perisoreus canadensis*) were qualitatively consistent with the model in most contexts (references above). However, because the model implicitly assumes that a hoarder's behavior is not influenced by that of other individuals, methodological measures were taken in those experiments to eliminate any confounding effects of social context on the jays' caching behavior.

Here, I describe a simple field experiment designed to investigate whether the distance to which Gray Jays transport food items for storage is affected by load (food-item) size and social context (solitary or in the company of one or more conspecifics). I present evidence that apparent attempts by the jays to cache secretively were influenced by the size (value) of the food item, the immediate risk of losing a cache to a conspecific soon after the cache had been put in place, and the interaction of these two factors (food-item size and social context). Any tendency to cache secretively may reduce the probability of cache theft, which may be accomplished also by adequately spacing caches (Waite 1988, Waite and Reeve 1992a), appropriately timing the decision to move on to alternative sources while a known source still contains food (Waite and Reeve 1992b), placing caches in inconspicuous sites (Petit et al. 1989, Waite 1991a), and concealing caches (Petit et al. 1989, Waite 1991a).

The Gray Jay is a permanent resident of high-latitude boreal forests in North America. These birds store hundreds of food items per day during summer (Waite 1991a), and apparently rely heavily on that food during the winter (Waite 1990), when they have as little as 4 hr of foraging time available each day during which to accumulate energy reserves for the upcoming night of hypothermic fasting (Waite 1991b, in press). Food items are cached as saliva-coated boli (Dow 1965), each of which is placed in a separate arboreal site, such as under a flake of bark, in a clump of lichen, or in a conifer needle-cluster.

METHODS

The study was conducted between 13 and 25 August 1986 in black spruce (*Picea mariana*) forest in the central Brooks Range, north-central Alaska (67°22'N, 150°08'W; see Waite and Reeve 1992b). Air temperature ranged from 16 to 23°C and no rainfall occurred during the experiment.

I tested three jays that together formed a social unit and held a territory. I had tamed these jays prior to the experiment by provisioning them with raisins. The social unit consisted of a mated pair and a single (putative male) juvenile. The jays were color-marked and, for convenience, will be referred to hereafter by their color combinations: white/white (w/w) = adult male, white/red (w/r) = adult female, and purple/yellow (p/y) = juvenile (probably at least four months post-fledging). This is the typical composition of a social unit on my study area; some territories have a fourth individual, an adult whose relatedness to the other members of the social unit is unknown. At my study area (unpubl. data), as well as in Ontario and Quebec (Strickland 1992) and the Yukon Territory (S. Hannon, in litt.; C. C. Shank, pers. comm.), it is typical for one juvenile to evict all of its subordinate siblings from the natal territory and to remain on that territory at least through the first winter. This form of delayed dispersal occurred in the present study: p/y evicted a putative sibling from the territory in June and then went on to spend the following winter on that territory.

The experiment was conducted by first whistling to attract at least one of the jays to an arbitrary location within the territory. When two or three of the jays arrived together, I randomly chose one of them to test. I then randomly determined whether to give that jay a one- or two-raisin bolus. Two-raisin boli were formed by manually compressing two raisins so that they stuck to each other. The jays cached such boli as single items. The raisins were offered from the palm of the hand to w/r and p/y, and by tossing them into the air to w/w, who was not hand-tamed but was adept at catching raisins in flight. After the jay had cached the bolus and returned to the source, I offered a second bolus to that jay. I then walked ~15 m in an arbitrary direction and offered two more boli. The rationale for presenting only two items at each location is based on previous work
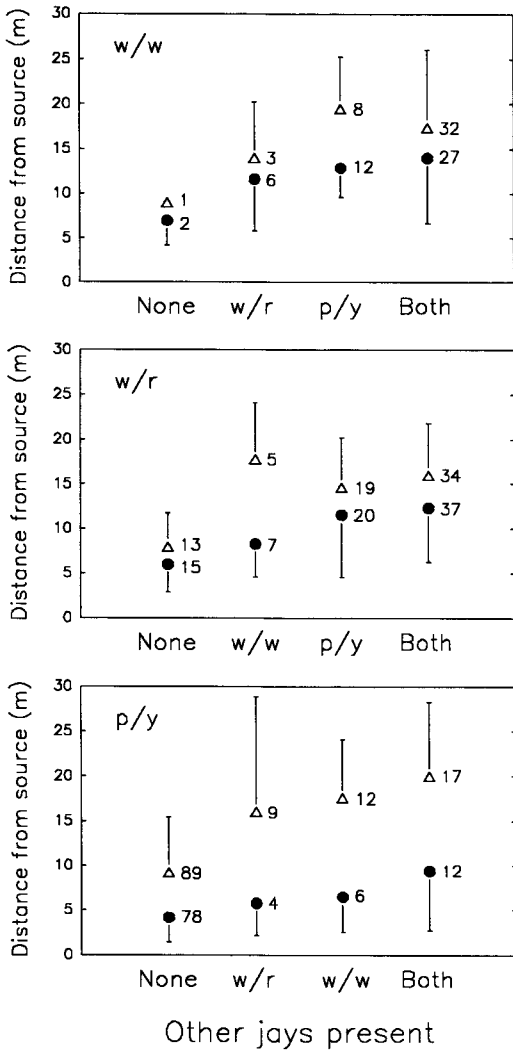
FIGURE 1. The relationship between social context and the distance to which food items were transported for storage by three Gray Jays (w/w, w/r, and p/y) storing one-raisin (filled circles) and two-raisin boli (open triangles). Symbols represent means, vertical lines represent 1 SD, and the numerals indicate the number of caching trips.

that showed a sequential increase in the distance items were transported for storage when a jay made multiple trips from a point source of food (Waite 1991a, Waite and Reeve 1992b). After offering raisins from four successive locations and except when the session was interrupted by the departure of the jay, I switched to one of the other two jays. When neither of those jays were in the vicinity, the procedure was repeated at a series of four additional locations with the same jay.

Each time a jay transported a bolus for storage, I recorded the identity of any other jays that were within

30 m of the source at any time during the interim between when the jay took the bolus from the source and when the jay had finished putting the cache in place and had departed from the cache site (usually to return to the source). For each caching trip, I also recorded the distance from the source to the storage site (measured to the nearest meter with an optical "tapemeasure"). In addition, I took records of supplanting attacks, attempted cache thefts, and avoidance of cache theft.

Because a repeated-measures analysis of variance was not feasible, I performed a two-way analysis of variance on the data for each of the three jays separately. In this design, I tested for effects of load size (one- vs. two-raisin bolus), social context (solitary, with one jay, with the other jay, or with both jays), and an interaction between those two factors. Because a separate analysis was performed for each of the three jays, to achieve "true" significance with the family comparison alpha level set at 0.05, nominal probabilities $\leq 0.05/3$ were considered significant (Bonferroni's inequalities method; Snedecor and Cochran 1980).

RESULTS

Figure 1 shows the relationship between load size and mean transportation distance for the four categories of social context. The jays tended to carry the large items to more distant sites for storage. This effect was significant in individuals w/r ($F_{1,142} = 16.088, P < 0.001$) and p/y ($F_{1,219} = 56.551, P < 0.001$), but not in w/w ($F_{1,83} = 1.722, P = 0.19$). The jays also tended to carry items farther from the source when they cached in the company of at least one other jay than when they cached alone. This effect too was significant in w/r ($F_{3,142} = 11.157, P < 0.001$) and p/y ($F_{3,219} = 20.174, P < 0.001$), but not in w/w ($F_{3,83} = 1.389, P = 0.25$). The failure to find a significant effect of either load size or social context for individual w/w may reflect the low power of the test owing to the small numbers of caching trips taken by that individual while it was solitary (see Fig. 1). Finally, while all three jays tended to show a greater difference in transportation distance for large versus small items when they were in the company of one or more of the other members of the social unit than when solitary, a significant interaction effect emerged between load size and social context for individual p/y only ($F_{3,219} = 3.571, P = 0.015$; test results for other individuals: $F_{3,83} = 0.294, P = 0.83$ [w/w], and $F_{3,142} = 1.299, P = 0.28$ [w/r]).

I observed seven obvious attempts by one jay to steal another jay's cache during the caching process or just after it had been completed (cf. Burnell and Tomback 1985). In each case, the jay attempting the theft flew directly to the immediate vicinity of the cache site either while the cacher was still present or just after the cacher had left the site. The would-be robber then engaged in an obvious search of the site, cocking its head to the side and sometimes probing the site with its bill. On only one occasion was a jay (w/w) successful in retrieving another jay's (w/r) recently made cache. In every other case, the cacher avoided losing the food in one of two ways. If the bolus had already been put in place, the cacher extracted the bolus as the supplanting jay approached, or the cacher actually re-

turned to the cache site and removed the cache before the other jay was able to find it. The cacher then flew to a more distant site where it recached the bolus. If the cacher was supplanted or approached before it had put the bolus in place, it simply flew to a more distant location and cached the bolus. Individual w/w was unsuccessful in a single attempt to steal one of p/y's caches. On four occasions, p/y made an obvious attempt to steal w/r's cache, and on one occasion tried to steal w/w's cache. These attempts by p/y to steal its putative parents' caches were accompanied by begging vocalizations and wing-quivering displays, both of which are characteristic behaviors of the prolonged period of parent-directed demand behavior by the juvenile that delays its dispersal from its natal territory (see above).

DISCUSSION

The significant effect of load size on the distance to which food was transported for storage (Fig. 1) corroborates the results of previous studies on the dispersion of caches in Gray Jays (Waite 1991a), European Jays (*Garrulus glandarius*; Bossema 1979), and in several species of squirrels that scatterhoard (fox squirrel, *Sciurus niger,* Stapanian and Smith 1984; red squirrel, *Tamiasciurus hudsonicus,* Hurly and Robertson 1987; gray squirrel, *S. carolinensis,* Jacobs 1987). Similar load size-distance relationships have been reported for a wide variety of central-place foragers engaging in non-caching behaviors in both single-prey and multiple-prey loading contexts (reviewed by Stephens and Krebs 1986). The present results are consistent with the rate-maximization model (Waite 1991a; Waite and Reeve 1992a, 1992b; but see below), which predicts, under most ecologically relevant conditions, that larger food items should be transported to more distant cache sites, where the density-dependent survivorship is likely to be higher (see Hurley and Robertson [1987] for an alternative view). These results show that Gray Jays incurred higher time and energy costs while storing the larger, more valuable food items.

That the jays tended to transport food items to more distant storage sites when other jays were nearby (Fig. 1) indicates that secretive caching may be an important means of protecting caches from theft (cf. Burnell and Tomback 1985). In fact, the effect of social context on transportation distance was pronounced. When caching small boli while solitary, the jays often cached in the closest available tree. Individual p/y, for instance, cached 31% of small boli within 2 m of the source while solitary, but only 11% within 2 m of the source while social (i.e., accompanied by at least one other jay). By contrast, the same individual cached <10% of small boli farther than 6 m from the source while solitary, and >40% farther than 6 m from the source while social. Only a few of the long distances traveled to store items while social were the direct result of overt avoidance by the cacher of another jay apparently attempting to rob the cache (see Results). Thus, most of the long caching trips made when other jays were present appear to represent a compensatory adjustment for a generally heightened risk of immediate cache theft. The magnitude of such adjustments may represent a compromise because if jays transport food to very distant cache

sites while other jays are near the source, they can minimize the immediate loss of caches to conspecifics, but the rate at which they store food will be low. To evaluate whether such compensation for social context is of the rate-maximizing magnitude will require the development and testing of a new formulation of our model, one in which social-context effects are incorporated. In any case, my results suggest that although the jays may often fly far enough from the source to cache without interference, when they do cache while conspecifics are relatively nearby, they may monitor the short-term survival of a cache and then recache it if a conspecific attempts to steal it (see also Pinkowski 1977, Tomback 1978, Brockmann and Barnard 1979). This latter course of action may usually result in a high probability that a cache will be recoverable by the cacher at some future time because Gray Jays have some capacity to remember the locations of their own caches (Bunch and Tomback 1986; see also Balda et al. 1987) but apparently not those caches made within their view by conspecifics (Bunch and Tomback 1986; see also Sherry et al. 1981, Vander Wall 1982, Baker et al. 1988).

The significant interaction effect between load size and social context in p/y (Fig. 1) reflects the tendency of that individual to cache at quite distant sites when social, particularly when transporting larger food items. This results indicates, at least for that individual, that the tendency to cache in secrecy increased with the value of the food item being cached.

Other studies on scatterhoarding behavior have examined how the presence of conspecifics may influence the amount of food stored (e.g., Stone and Baker 1989; see also Vander Wall 1990) and the pattern of cache dispersion (e.g., Cowie et al. 1981, Stapanian and Smith 1978, Clarkson et al. 1986, Covich 1987, Woodrey 1989). The results of this preliminary study begin to show the importance of social constraints on cache-spacing behavior, an aspect of scatterhoarding behavior that until now has received virtually no attention (but see Covich 1987). Much theoretical and empirical work will be necessary to elucidate the complexities of the effects of sociality on the caching behavior of Gray Jays and other group-living scatterhoarders. It will be of particular interest to examine any role social dominance may play, and whether parental/mate investment and kinship effects are important.

LITERATURE CITED

BAKER, M. C., E. STONE, A. E. BAKER, R. J., SHELDON, P. SKILLICORN, AND M. D. MANTYCH. 1988. Evidence against observational learning in storage and recovery of seeds by Black-capped Chickadees. Auk 105:492–497.
BALDA, R. P., K. G. BUNCH, A. C. KAMIL, D. F. SHERRY, AND D. F. TOMBACK. 1987. Cache site memory

in birds, p. 645–666. *In* A. C. Kamil, J. Krebs, and H. R. Pulliam [eds.], Foraging behavior. Plenum Press, New York.

BOSSEMA, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70:1–117.

BROCKMANN, H. J., AND C. J. BARNARD. 1979. Kleptoparasitism in birds. Anim. Behav. 27:487–514.

BUNCH, K. G., AND D. F. TOMBACK. 1986. Bolus recovery by Gray Jays: an experimental analysis. Anim. Behav. 34:754–762.

BURNELL, K. L., AND D. F. TOMBACK. 1985. Steller's Jays steal Gray Jay caches: field and laboratory observations. Auk 102:417–419.

CLARKSON, K., S. F. EDEN, W. J. SUTHERLAND, AND A. I. HOUSTON. 1986. Density dependence and Magpie food hoarding. J. Anim. Ecol. 55:111–121.

COVICH, A. P. 1987. Optimal use of space by neighboring central place foragers: when and where to store surplus resources. Adv. Behav. Econ. 1:249–294.

COWIE, R. J., J. R. KREBS, AND D. F. SHERRY. 1981. Food storing by Marsh Tits. Anim. Behav. 29:1252–1259.

DOW, D. D. 1965. The role of saliva in food storage by the Gray Jay. Auk 82:139–154.

HURLY, T. A., AND R. J. ROBERTSON. 1987. Scatterhoarding by territorial red squirrels: a test of the optimal density model. Can. J. Zool. 65:1247–1252.

JACOBS, L. F. 1987. Food-storing decisions in the gray squirrel (*Sciurus carolinensis*). Ph.D.diss., Princeton Univ., Princeton, NJ.

PETIT, D. R., L. J. PETIT, AND K. E. PETIT. 1989. Winter caching ecology of deciduous woodland birds and adaptations for protection of stored food. Condor 91:766–776.

PINKOWSKI, B. C. 1977. Food storage and re-storage in the Red-headed Woodpecker. Bird-Banding 48: 74–75.

SHERRY, D. F., J. R. KREBS, AND R. J. COWIE. 1981. Memory for the location of stored food in Marsh Tits. Anim. Behav. 29:1260–1266.

SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods. Iowa State Univ. Press, Ames, IA.

STAPANIAN, M. A., AND C. C. SMITH. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. Ecology 59:884–896.

STAPANIAN, M. A., AND C. C. SMITH. 1984. Density-dependent survival of scatterhoarded nuts: an experimental approach. Ecology 65:1387–1396.

STEPHENS, D. W., AND J. R. KREBS. 1986. Foraging theory. Princeton Univ. Press, Princeton, NJ.

STONE, E. R., AND M. C. BAKER. 1989. The effects of conspecifics on food caching by Black-capped Chickadees. Condor 91:886–890.

STRICKLAND, R. D. 1992. Juvenile dispersal in Gray Jays: dominant brood member expels siblings from natal territory. Can. J. Zool. 69:2935–2945.

TOMBACK, D. F. 1978. Foraging strategies of Clark's Nutcracker. Living Bird 16:123–161.

VANDER WALL, S. B. 1982. An experimental analysis of cache recovery in Clark's Nutcracker. Anim. Behav. 30:84–94.

VANDER WALL, S. B. 1990. Food hoarding in animals. Univ. of Chicago Press, Chicago.

WAITE, T. A. 1988. A field test of density-dependent survival of simulated Gray Jay caches. Condor 90: 247–249.

WAITE, T. A. 1990. Effects of caching supplemental food on induced feather regeneration in wintering Gray Jays *Perisoreus canadensis*: a ptilochronology study. Ornis Scand. 21:122–128.

WAITE, T. A. 1991a. Economics and consequences of scatterhoarding in Gray Jays (*Perisoreus canadensis*). Ph.D.diss., Ohio State Univ., Columbus, OH.

WAITE, T. A. 1991b. Nocturnal hypothermia in Gray Jays *Perisoreus canadensis* wintering in interior Alaska. Ornis Scand. 22:107–110.

WAITE, T. A. In press. Winter fattening in gray jays: seasonal, diurnal and climatic correlates. Ornis Scand.

WAITE, T. A., AND J. D. REEVE. 1992a. Gray Jay scatterhoarding behavior, rate maximization, and the effect of local cache density. Ornis Scand. 23: 175–182.

WAITE, T. A., AND J. D. REEVE. 1992b. Caching behaviour in the Gray Jay and the source-departure decision for rate-maximizing scatterhoarders. Behaviour 120:51–68.

WOODREY, M. A. 1989. Caching behavior and ecology of free-ranging White-breasted Nuthatches (*Sitta carolinensis*). M.Sc.thesis, Ohio State Univ., Columbus, OH.