A FIELD TEST OF DENSITY-DEPENDENT SURVIVAL OF SIMULATED GRAY JAY CACHES[1]

THOMAS A. WAITE
Department of Zoology, The Ohio State University, Columbus, OH 43210

Gray Jays (*Perisoreus canadensis*) cache surplus food extensively during summer and opportunistically at other times of the year. Food items are cached as saliva-coated boli (Dow 1965). Each bolus is cached above ground and in a separate site, such as in a bark crevice, in coniferous foliage, or in a fork between twigs. These caches are used during winter (pers. observ.) and through the following breeding season in March and April, when food supplies can still be reduced and not yet replenishing (Strickland unpubl., cited in Sherry 1985). Unlike animals that larderhoard (e.g., pine squirrels, *Tamiasciurus douglasii,* Smith 1970; Acorn Woodpeckers, *Melanerpes formicivorus,* MacRoberts and MacRoberts 1976; pocket mice, *Perognathus intermedius,* Reichman and Fay 1983), Gray Jays scatter their caches, as do other corvids (Goodwin 1976, Ligon 1978, Vander Wall and Balda 1981, Tomback 1982, James and Verbeek 1983, Clarkson et al. 1986). Gray Jays and Siberian Jays (*Perisoreus infaustus,* Blomgren 1964), however, differ from other corvids in that they cache in trees rather than on the ground.

The strategy of scatterhoarding renders individual caches indefensible against pilferage by competitors, such as Gray Jays from adjacent territories. A Gray Jay transporting food from a central point to surrounding cache sites might be expected to achieve a spatial distribution of caches that represents a trade-off between the benefit of reduced cache robbery (i.e., reduced density-dependent loss of caches to competitors which are naive to the cache locations) and time and energy costs of longer flights required to achieve low densities. Because Gray Jays have some memory for the locations of their caches (Bunch and Tomback 1986), placing caches in widely separated sites should discourage competitors without making it too difficult to find their own caches. Although much of the food eaten and cached by Gray Jays typically is not clumped (Strickland, unpubl.), jays have been observed making caching trips radiating from central food sources such as animal carcasses (e.g., red fox, *Vulpes fulva,* Ouellet 1970; arctic ground squirrel, *Citellus parryi,* and red squirrel, *Tamiasciurus hudsonicus,* pers. observ.) and patches of blueberries (*Vaccinium* sp.; pers. observ.). Thus, it seems reasonable to apply to Gray Jays two models that have been developed to describe the eco-

nomics of transporting food from a central place to surrounding cache sites (Stapanian and Smith 1978, Clarkson et al. 1986). Though these models generate somewhat different predictions, they share the assumption that survivorship of caches decreases with increasing cache densities. In this paper I present a test of this assumption applied to simulated Gray Jay caches. To the extent that this assumption holds, Gray Jays might be predicted to balance the benefit of spacing their caches widely (i.e., a high probability that the caches will survive long enough to be recovered) against the costs required to place caches at low densities.

METHODS

The experiment was conducted in a white spruce (*Picea glauca*) forest near Haines Junction, Yukon Territory, Canada (60°46′N, 137°20′W) between 29 August and 16 September 1984. In each of three imaginary cylinders with radii of 1, 3, and 6 m, I placed 10 raisins between 1 and 2.5 m above ground in live needles in white spruce (*P. glauca*) trees. I attempted to space the raisins as evenly as possible given the constraint of availability of appropriate cache sites. Thus, I made artificial caches at three densities: high (~2.12 raisins m^{-3}), intermediate (~0.24 raisins m^{-3}), and low (~0.06 raisins m^{-3}). All raisins were cached from 1 to 4 m from the trunk of a white spruce in microsites closely simulating the cache sites of Gray Jays. Each of four such replicates was conducted in a distinct Gray Jay territory as determined previously by observing territorial disputes between adjacent social units. Two of the social units were comprised of two adults and one juvenile, the third had three adults and one juvenile, and the fourth had two adults and no juveniles. These jays presumably were mated pairs and offspring, although the supernumerary adult in the third social unit might have been a nonrelative (Strickland, unpubl.). All these jays were semitame and had been offered raisins before the experiment. The cylinder locations within each territory were randomized, with the constraint that the three cylinders of each replicate were separated from one another by at least 35 m. In all cylinders, raisins were cached among the needled portions of at least two adjacent trees. To avoid inadvertently cuing jays to the locations of raisins, I used no markers but instead recorded detailed descriptions of cache locations to facilitate finding my own caches. Also, to minimize the possibility of jays watching while I made caches, I placed the raisins at dusk, after the jays had gone to roost. Although I never observed any animal other than a Gray Jay removing any of my artificial caches, it is conceivable that not all caches
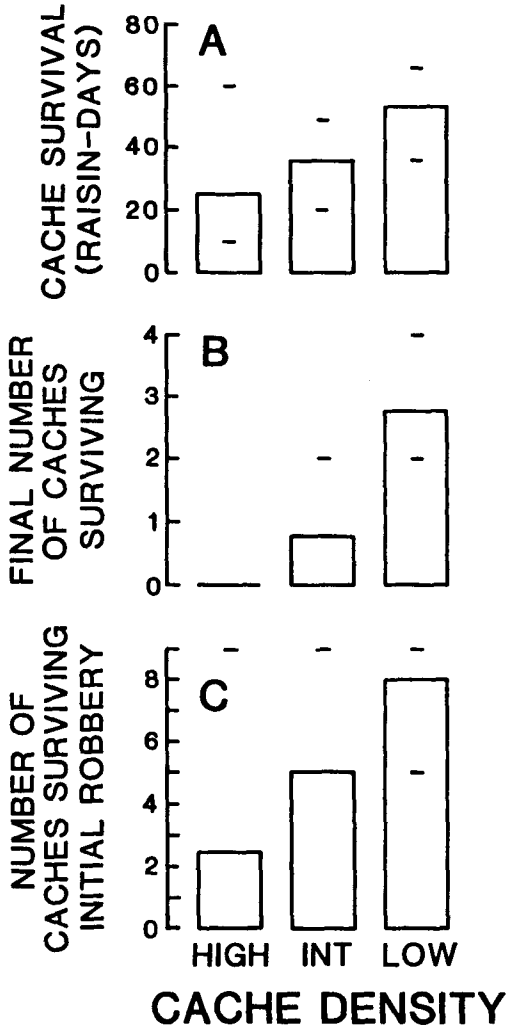
FIGURE 1.   Survival of 10 raisins artificially cached at three densities: high ($\sim$2.12 m^{-3}), intermediate ($\sim$0.24 m^{-3}), and low ($\sim$0.06 m^{-3}). Bars represent the means and short horizontal lines indicate the ranges ($n = 4$ replicates). (A) Summation, over 10 days, of the number of raisins surviving at the end of each day. (B) Number of raisins surviving at the end of the 10th day. (C) Number of raisins surviving at the end of the first day on which at least one cache was robbed.

were robbed by jays. Black-billed Magpies (*Pica pica*) and red squirrels (*Tamiasciurus hudsonicus*), both of which are also diurnal, occurred in the study area and might have removed some of my caches. Survival of the cached raisins was checked daily at dusk for 10 days.

Two measures of cache survival were used, raisin-days (1 raisin-day = the survival of 1 raisin for 1 day) and number of raisins surviving 10 days. Statistical

analysis of cache survival was accomplished by Jonck-heere's (J) test for ordered alternatives (Hollander and Wolfe 1973). J-values with probabilities $\leq$0.05 were considered statistically significant. One-tailed tests were used to examine the a priori predictions that (1) the number of raisin-days and (2) the number of raisins surviving 10 days would be higher in cylinders of lower initial cache densities, and (3) the number of raisins robbed from a cylinder on the first day on which at least one was removed would be higher in cylinders of higher initial cache densities.

RESULTS AND DISCUSSION

The survival of cached raisins was significantly higher at lower cache densities both in raisin-days (J = 38, $P = 0.023$, one-tailed, Fig. 1A) and in number of raisins surviving 10 days (J = 43, $P = 0.004$, one-tailed, Fig. 1B). That none of the raisins cached at the highest density survived in any of the four replicates indicates that placing caches too close to one another may increase their vulnerability to pilferage by competitors naive to the cache sites.

I indirectly tested whether the probability of naive competitors engaging in an "area-restricted search" (sensu Stapanian and Smith 1978, Sherry et al. 1982) after making an initial chance find of another individual's cache was related to the initial cache density. I reasoned that if this were the principal reason for lower survivorship of caches at higher initial densities, then more caches might be removed from cylinders of higher cache densities on the day of the initial chance find. Thus, I compared across the different-sized cylinders the number of caches surviving at the end of the first day on which at least one cache was pilfered. Significantly more caches were robbed in cylinders of higher cache density (J = 36.5, $P = 0.046$, one-tailed, Fig. 1C). However, a statistically significant relationship did not emerge between the latency to initial cache pilferage (days) and initial cache density (J = 32.5, $P > 0.10$, two-tailed). This finding suggests that caches at low densities survived better not solely because they were more likely to escape an initial chance find. The above results, taken together, support the conclusion that caches survived better at lower densities because competitors were less likely to persist in an area-restricted search after finding a single cache by chance. On one occasion, I was able to watch a Gray Jay engaging in such a search after finding one of my artificial caches in a cylinder of intermediate cache density. After transporting the first raisin $\sim$20 m to a new cache site, the solitary jay repeatedly returned to the vicinity of the first find and in $\sim$7 min removed and redistributed seven of the 10 raisins from that cylinder.

My results corroborate the results of similar tests of density-dependent survivorship with simulated caches of other scatterhoarders, Marsh Tits (*Parus palustris*; Sherry et al. 1982), fox squirrels (*Sciurus niger*; Stapanian and Smith 1984), and magpies (Clarkson et al. 1986), but see Kraus (1983). Although the initial densities of artificial caches in this experiment, even in the low-density cylinders, might have been somewhat higher than is typical for Gray Jay caches, the results, nevertheless, demonstrate the importance of spacing caches adequately so that competitors naive to their

locations will be discouraged from engaging in a persistent, systematic search in the vicinity of an initial chance find. In fact, because the rate of density-dependent cache pilferage should be partly a function of the length of time food is left in storage (Clarkson et al. 1986), the low survivorship of caches over only 10 days in the present experiment suggests that food cached in summer to be used in winter should be placed at densities considerably lower than those I used. In any case, my results indicate that Gray Jays which make hoarding trips radiating from a central concentrated food source might be expected to balance the benefit of low cache densities (i.e., high cache survivorship) against the costs of the longer flights required to achieve those densities (Stapanian and Smith 1978; Clarkson et al. 1986, unpubl. results).

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WEDDELL SEAL PREYS ON CHINSTRAP PENGUIN[1]

FRANK S. TODD
Sea World Research Institute/Hubbs Marine Research Center,
1720 South Shores Rd., San Diego, CA 92109

Key words: Predation; Weddell seal; Chinstrap Penguin.

Some species of pinnipeds regularly prey upon penguins. In my experience, these include leopard seal (Hydrurga leptonyx), Kerguelen fur seal (Arctocephalus

gazella), Hooker's sea lion (Phocarctos hookeri), and South American sea lion (Otaria flavescens). This behavior has not been previously reported in Weddell seals (Leptonychotes weddelli), a relatively docile species which typically inhabits the fast-ice zone of the high Antarctic, and feeds primarily on fish.

Between 5 and 8 December 1986, I was camped in Harmony Cove (62°19'S, 59°15'W), Nelson Island, South Shetland Islands. Ice and snow conditions were far more extensive than I had seen there previously.