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Walnut-caching behavior of American Crows

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ABSTRACT. Each autumn, American Crows (*Corvus brachyrhynchos*) in the Central Valley of California, USA, forage heavily on walnut trees (*Juglans regia*) planted along residential streets. Some of these nuts are dropped onto roads and cracked for immediate consumption, but others are carried away from foraging sites to be cached. I quantified caching behavior to understand its importance in corvid natural history and the potential for corvids to disperse large tree seeds. Crows cached an estimated 2000 walnuts/km^2/yr in agricultural fields 1–2 km away. Most (73%) crows that found a walnut left the foraging site with it, and most (77%) of these crows cached their nuts. Some crows carried walnuts long distances (e.g., 5% of nuts foraged from trees were carried >2 km) and buried them in unforested habitat; this indicates that crows may be agents of tree seed dispersal. Transporting and caching a nut required approximately 10 min and increased the likelihood of it being stolen, relative to a nut eaten immediately at the walnut tree. Without knowing the timing and rates of recovery, it is unclear when and to what degree American Crows benefit from walnut-caching, which has not been previously described in this species.

SINOPSIS. **Conducta de cargar y transportar nueces de parte de *Corvus brachyrhynchos***

Cada otoño individuos del cuervo (*Corvus brachyrhynchos*) forrajean en árboles de nueces (*Juglans regia*), que son plantados a lo largo de zonas residenciales en el valle central de California. La aves dejan caer algunas de las nueces para que se rompan e ingerir su contenido. Sin embargo, otros cuervos cargan en su pico y transportan las nueces a otras localidades. Cuantificamos la conducta de transportar nueces para tratar de entender la importancia de esta conducta en los cuervos y el potencial de dispersión de las semillas. Los cuervos cargan la nueces de 1–2 kms y un estimado de 2000 nueces/km cuadrado al año en áreas agrícolas. El 73% de los cuervos se llevan las nueces que encuentran y el 77% las transportan. Algunas aves llevan las nueces grandes distancias (5% más de 2 kms) y las entierran en localidades sin árboles. Esto es un indicativo de que los cuervos son agentes de dispersión. El cargar y transportar una nuez requiere unos 10 minutos y aumenta la probabilidad de que sea robada, en comparación con aquellas aves que consumen la nuez en el árbol o sus inmediaciones. No podemos indicar con claridad el grado de beneficio de los cuervos que cargan las nueces (conducta previamente no descrita), si no conocemos el tiempo de recobro.

Key words: American Crow, caching, *Corvus brachyrhynchos*, hoarding, walnut

Crows and other corvids are among the most familiar of birds, and their habit of hiding valuable items is legendary (Goodwin 1976). Surprisingly, there is little detailed information available on caching by American Crows (*Corvus brachyrhynchos*), despite their common occurrence in human-dominated landscapes. Detailed descriptions of caching behavior are available for two related species: walnut-caching by Rooks (*C. frugilegus*, Källander 1978), and mollusk-caching by Northwestern Crows (*C. caurinus*, James and Verbeek 1983). I studied caching of English walnuts (*Juglans regia*) by American Crows in a small city in a nut-growing region of California's Central Valley. Residential streets in this region are commonly lined with walnut trees. In early autumn, American Crows cached walnuts that they had removed from trees by prying loose their soft outer husk. Later, they cached nuts that had naturally lost their husks and fallen to the ground. Walnuts that were not cached were eaten immediately after being opened by repeated dropping on asphalt streets or hard-packed soil in fallow agricultural fields (Cristol and Switzer 1999). Crows cached less-preferred walnuts (e.g., smaller, uncracked) and immediately consumed the more preferred nuts (Cristol 2001). The objective of this study was to quantify the occurrence of walnut-caching by crows in an effort to understand the costs and benefits of this behavior. These data should also serve as a baseline for predicting the impact of crows on nut tree dispersal and as a basis for comparative studies on avian caching behavior.

METHODS

I observed crows foraging on walnut trees in Davis, Yolo County, California. All observa-

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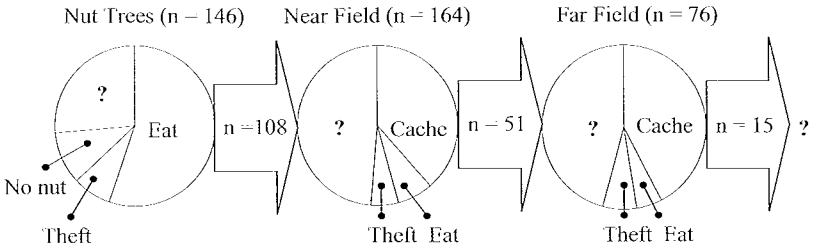

Fig. 1. Schematic diagram of the fate of nuts foraged by American Crows at walnut trees or after transport to agricultural fields 1–2 km away. Arrows show how many nuts were transported away from the site. Question marks indicate fate unknown.

tions were made from September through November 1995, between dawn and 11:00 PST, because preliminary observations indicated that crows did not cache walnuts in the afternoon or evening. The numbers of foraging and caching crows varied from approximately 100 individuals to more than 1000. Pilot studies indicated that crows behaved similarly at nine sites in Davis, but all data presented here are for a cluster of 10 walnut trees along one block of Birch Lane.

Crows leaving Birch Lane with walnuts in their beaks were followed on bicycle to where they landed in agricultural fields up to 2 km away and observed with 10× binoculars or a 15× spotting scope. I made 146 observations of birds foraging in walnut trees on nine mornings between 18 September and 23 October. To increase the sample size for birds arriving at the agricultural fields, I observed 240 arrivals of birds carrying nuts from Birch Lane on 14 mornings between 28 September and 30 October. Whenever possible, birds were followed until they returned to the source trees. In addition, I estimated the rate at which crows transported walnuts from Birch Lane to nearby fields using a separate set of data; from a distant vantage point I counted crows entering the nearest agricultural field from the Birch Lane nut trees for 330 min on three mornings between 25 and 28 September.

To determine if caching might dry out the nut shells and reduce the amount of work required to break them after retrieval, I simulated caching and then dropped the experimentally stored and fresh walnuts to compare breakability. I gathered 80 nuts from an English walnut tree, removed the husks, and stored them indoors at ~16°C with negligible humidity, covered with a small amount of dry soil from an agricultural field for 30 d to simulate caching. After 30 d the nuts had stopped losing mass, and so I reasoned that longer caching would have no further effect on breakability. (It should be noted that little is known of cache duration or microclimate preference, so the conditions chosen for the simulated caching were established by guesswork.) I then picked 80 more fresh nuts from the same tree and removed their husks for a comparison of breakability. I dropped 20 nuts of each treatment (stored or fresh), on the day the fresh nuts were picked, from each of four heights (1.5, 3, 6, and 9 m) onto asphalt. The rationale for choosing these heights was that they spanned the range of heights commonly used by crows at this site. Each nut was dropped repeatedly from the same height until a hole >1 cm^2 had been formed in the shell, and the number of drops recorded. ANOVA was used to compare the effects of treatment and drop height on the number of drops required to break the nuts. Throughout the text all mean values are accompanied by standard deviation.

RESULTS

Of 146 instances of crows observed foraging in walnut trees at Birch Lane, none resulted in nuts being cached on site (although caching was observed casually there on a few occasions). Most foragers (73%) flew with a nut directly to surrounding agricultural fields, where nuts were cached, eaten, or stolen (Fig. 1). Birds that did not leave with a walnut either ate their nut at Birch Lane (15%, this category includes those nuts abandoned after opening by dropping), lost nuts to theft by other crows (2%), left Birch Lane with no nut (3%), or could not be observed (7%).

Whenever possible, I followed crows that flew from Birch Lane with walnuts to the nearest agricultural field (centered 1 km away). Many of 164 arrivals over the fields did not stop (31%); rather they continued transporting their nut into the vast area of agricultural fields to the north. Those that did stop in the first field ($N = 113$) generally cached their nuts under soil and dried vegetation (38%), while the remainder ate their nuts on the ground (7%), lost their nuts to theft by other crows (5%), or were lost from view (50%; Fig. 1). The high percentage of nuts with unknown fates was a result of the fact that I was observing the birds from up to 1 km away, and they transported nuts for up to 10 min. If I lost sight of a bird, even momentarily during this time, it was classified as lost from view because I could no longer be sure it was the same bird or carrying the same nut.

Some of the crows that continued north of the field closest to Birch Lane were followed to a more distant agricultural field centered approximately 2 km from Birch Lane. Of 76 birds crossing over this field with nuts, only 20% continued flying farther (Fig. 1). Of the 61 birds landing in this field, 43% cached their nuts, 5% ate their nuts, 6% lost nuts to theft by other crows, and 46% landed in weeds and were lost from view before fate of the nut was determined.

Combining the focal observations from Birch Lane and the fields 1 and 2 km away reveals that at least 5% of nuts removed from trees were carried >2 km away (combined probabilities of birds carrying nuts from each location: $0.73 \times 0.31 \times 0.20$). Caching was the most likely fate for a nut that was transported to surrounding agricultural fields (77% of 90 nuts for which fate was determined). The remaining transported nuts were either eaten (12%) or stolen before caching (11%).

Transporting nuts to agricultural fields and caching them required considerable time. On average (±SD), a crow caching in one of the agricultural fields required 166 (±141) s ($N = 40$) to reach a caching location in the nearest agricultural field, an additional 106 (±61) s ($N = 55$) to bury the nut, and 313 (±129) s ($N = 16$) to return to the source trees, or nearly 10 min to transport and cache a single walnut in the nearest field. The time required to return was longer than the outward journey, because crows often stopped several times on their return, for example, to chase another crow that was attempting to eat a walnut (D. A. Cristol, unpubl. data). Many crows spent much more time transporting nuts because they flew to more distant locations. It was not unusual to observe a crow flying north with a walnut for >10 min until it disappeared on the horizon. Although it is not known whether these birds eventually cached their nuts, it seems likely since this was by far the most common fate of transported nuts in the nearer fields.

Table 1. Number of drops onto asphalt required to break walnuts picked fresh from tree or stored to simulate caching.

Drop height	Treatment	Mean ± SD	Difference
1.5 m	Stored	10.30 ± 4.91	1.15 drops
	Fresh	11.45 ± 4.21	
3 m	Stored	3.25 ± 0.97	1.55 drops
	Fresh	4.80 ± 1.24	
6 m	Stored	1.35 ± 0.59	0.85 drops
	Fresh	2.20 ± 0.41	
9 m	Stored	1.05 ± 0.22	0.75 drops
	Fresh	1.80 ± 0.77	

Based on counts from a distant vantage point, crows transported walnuts into the nearest agricultural field at a rate of 1.17 nuts/min. Based on the findings above, in which at least 43 (26%) of 164 nuts taken into the nearest field were cached, nuts were being cached at an estimated rate of >10 nuts/h/km^2 during the morning hours. (This estimate was arrived at by assuming that 26.2 % of the 70.2 nuts arriving in the 1.6 km^2 field each hour were cached: $0.26 \times 70.2/1.6$ km^2 = 11.41 nuts/h/km^2). This number is an underestimate because an unknown fraction of the birds lost from view or seen flying farther also cached eventually. Conservatively estimating that crows cached for 4 h/day during the peak walnut ripening period from 15 September to 30 October, crows were burying approximately 2000 nuts/km^2/yr.

Walnuts that had been stored indoors in dry soil for 30 d to simulate the effects of caching on breakability broke after one less drop than fresh nuts dropped from the same heights (mean difference for all heights combined = 1.07 drops; Table 1). Despite the apparent difference in mean drops required, there was no

significant effect of the storing treatment on breakability (whole model, $F_{3,156} = 54.06$, $P < 0.0001$; treatment, $F_1 = 2.23$, $P = 0.14$; height, $F_1 = 157.39$, $P < 0.0001$; no significant interaction).

I did not record quantitative data on the different motor patterns comprising nut-hiding behavior. A qualitative description follows. After crows landed they walked for up to 100 m, usually on top of the ridge of soil produced by the plough, apparently inspecting potential sites. With little warning they then poked their bill, containing the nut, quickly under 1–2 cm of soil or a dried tomato plant left from the previous year's harvest. Often, but not always, dirt or vegetation was placed quickly over the cache hole. Crows appeared to scan the area before flying off. Nuts were occasionally retrieved immediately and moved to nearby sites, sometimes because a potential thief had approached. If I approached a cache site while a crow was still present, it vocalized and appeared alarmed.

DISCUSSION

American Crows are known to cache food, but previous reports have been anecdotal and/or on territorial birds during the breeding season (Verbeek and Caffrey 2002). Nut caching during the non-breeding season by Rooks appears to be similar to that described here, in terms of the motor pattern involved and the potential ecological impact (Turcek and Kelso 1968; Purchas 1975; Källander 1978, 1997). In Lund, Sweden, Rooks also transported walnuts approximately 2 km and cached them in agricultural fields surrounding a city, at a peak rate of 41 nuts/h/km^2 (calculated from Källander 1978).

I occasionally observed crows retrieving cached walnuts throughout the study period, but I never knew how long the retrieved nut had been stored. Further study will be required to determine typical cache duration and recovery rates; without such information it is impossible to determine the benefits of caching. Intact walnuts remain fresh for at least several years if they do not germinate, while cracked nuts last only a few days before decay begins (D. A. Cristol, pers. obs.). Crows were occasionally observed caching partly eaten walnuts that would have decayed had they been cached for long (9% of 76 cached nuts, D. A. Cristol, unpubl. data). This suggests that crows may have been making some short-term caches. Other large corvids retrieve nuts several months or more after caching (e.g., Purchas 1975; Waite 1985; Tomback 1998), but short-term caching of perishable items has also been widely reported (Vander Wall 1990). Short-term caching of clams by Northwestern Crows involved similar motor patterns, but the highly perishable clams were generally retrieved within 24 h when the rising tide reduced food availability (James and Verbeek 1983).

Because animals often do not retrieve all of their caches (Vander Wall 1990), the annual burial of almost 2000 seeds/km^2 at a distance of 1–2 km from parent trees could have a large impact on seed dispersal, particularly in a less disturbed habitat than the one I studied. Because a housing development and golf course was constructed over the entire study site the year after this study, I have no data on germination success of unretrieved walnuts.

The finding that crows devote a large amount of time and energy to caching walnuts raises the question of the adaptiveness of the behavior. In general, caching should evolve in systems in which the caching individual has a greater fitness gain from the activity than non-caching individuals, and when the energetic benefits outweigh the energetic costs (but see Källander and Smith 1983). However, identifying the specific benefit of caching a walnut, as opposed to eating it immediately, is not straightforward, particularly in the absence of information on cache duration. If caches are retrieved many months later, when walnuts are no longer available and perhaps other food is in short supply, the advantages of caching excess walnuts in a time of plenty seem obvious. But there are other, less obvious potential benefits of caching.

Animals might cache food to reduce the chance of immediate theft by conspecifics present at a crowded foraging site. However, in this study crows did not reduce the immediate risk of loss to conspecifics when they carried walnuts 1–2 km away and cached them. Transported nuts had more than a five-fold greater chance of being lost to theft before caching or consumption than nuts consumed near the walnut trees (11% stolen in fields versus 2% stolen at trees). This occurred despite the fact that

crows were far less concentrated in the agricultural fields than at the walnut trees, where large numbers of birds harassed most foragers. Also, this does not include the expected losses caused by pilfering of nuts after caching. Thus, theft avoidance is unlikely to have been a selective force causing caching in this context.

A second possibility is that certain types of food may become more palatable after caching, increasing the value of a food item if it is cached as opposed to eaten immediately (akin to the breakdown of tannins in acorns; Fleck and Woolfenden 1997; cf. Hadj-Chikh et al. 1996). One could hypothesize an analogous situation in the present system: crows bury walnuts until their shells have dried and become easier to break, thereby reducing the energy required to consume them and increasing the energetic gain from each walnut. However, when I simulated caching for one month, the number of drops required for a nut to break experimentally was reduced by only one drop. Crows foraging naturally on nuts at source trees dropped them up to 16 times to crack them open, but on average only 1.4 drops were required. Since a nut must be dropped at least once to crack it, the maximum savings a crow could generate by caching is very small. Even if crows were to somehow reduce by one drop the work required to open a nut, energetically, this is a savings of only 0.2 kcal, as determined from Zach (1979), who estimated the energy required for *C. caurinus* to drop a small mollusk. Since crows typically flew >1 km to cache a walnut, which would require an extra expenditure of approximately 0.6 kcal, caching a nut for one month and thereby reducing the number of drops required to break it could not offset the expenditure required to transport it, based on the flight cost estimated by Bernstein et al. (1973) for Fish Crows (*C. ossifragus*). A food-preparation explanation might be plausible at sites requiring little or no transport to caching areas, for example, for territorial crows storing food near a nest, but it does not explain why these crows were transporting nuts great distances and caching them.

In conclusion, American Crows collectively transported large quantities of walnuts and buried them in treeless fields. These observations demonstrate for the first time that caching can be an important activity for this species during the non-breeding season and that crows could be important seed dispersers for nut-producing trees in a more natural environment. Their caching behavior closely resembled that of Rooks caching walnuts in Sweden and to a lesser extent that of Northwestern Crows caching mollusks in Canada. Caching at a distant site did not reduce the probability of theft or the amount of work required to open a walnut when compared to immediate consumption, and I can offer no satisfactory explanation for why American Crows cache walnuts. It is possible that walnut-caching behavior by crows is not adaptive in this highly disturbed agricultural habitat. Future studies should focus on the timing of cache retrieval with respect to food availability to determine whether crows that cache nuts benefit from the behavior in the short- or long-term.

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