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American crows cache less preferred walnuts

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Animals that can cache food are faced with the options of hiding or eating each food item they encounter. Empirical evidence from a few bird and mammal species suggests that the likelihood of caching may be influenced by a number of factors, including perishability, handling time, food value and the presence of potential cache robbers. American crows, *Corvus brachyrhynchos*, forage in large flocks for walnuts, and each nut must be either eaten immediately or transported elsewhere for caching. To examine which factors influence caching behaviour in this species, I observed free-living crows foraging for two species of walnuts at naturally occurring and provisioned sites, and documented characteristics of preferred and less preferred walnuts in dichotomous choice tests. The majority of crows flew off with their nuts and cached them in agricultural fields 1–2 km away, but others stayed near the walnut trees and cracked their nuts open by dropping them repeatedly on the ground. Nuts that were transported to agricultural fields and cached were significantly smaller than those eaten on site, indicating that crows were being selective about whether to consume or cache nuts. In dichotomous choice tests crows preferred English over black walnuts, which is unsurprising as English walnuts have higher energy value and are easier to crack. When choosing within-nut species, crows preferred cracked over intact and large over small nuts, also consistent with preferences based on minimizing handling costs or maximizing energy content. When provisioned with nuts of different species, sizes and condition (intact or slightly cracked), crows were more likely to cache black and intact walnuts. They were also more likely to cache nuts later in the day. When they did cache the more preferred English walnuts, crows spent more time hiding each nut. These results suggest that crows consumed preferred nuts immediately and cached less desirable nuts.

Many animals cache food for later consumption. Because food caching has implications for various aspects of behavioural ecology, such as interspecific competition and coevolution between seed cachers and food plants, it is important to understand why animals eat one food item and cache another (Vander Wall 1990). Numerous factors can influence the decision to cache, with perishability, handling time, food value and kleptoparasitism frequently cited as likely influences, but little consensus exists over which factors should be important under various circumstances (e.g. Carrascal & Moreno 1993; Hadj-Chikh et al. 1996; Heinrich & Pepper 1998). For example, when the handling time associated with eating a food item is long, captive squirrels cache less valuable items, as predicted by Jacobs (1992). In another situation, free-living nuthatches show the opposite behaviour, eating less preferred intact sunflower seeds and caching preferred seeds from which husks had been removed by a researcher (Woodrey 1990). The objective of this study was to determine whether free-living crows chose to cache or eat preferred food items when feeding on walnuts.

Western American crows, *Corvus brachyrhynchos hesperis*, forage heavily on two species of walnuts (English, *Juglans regia*, and northern California black, *J. hindsii*) in the Central Valley of California, U.S.A. Handling time is considerable because walnuts have a nearly impenetrable bony pericarp (hereafter 'shell') and, unless already cracked, require repeated drops against a hard surface to open (Cristol & Switzer 1999). Walnuts are suitable for long-term caching because when the shell is intact they are essentially nonperishable if stored in dry soil. English and black walnuts differ in nutritional value and handling time, and both vary greatly in size, providing numerous possible variables that could affect caching behaviour.

I first observed crows caching naturally occurring walnuts to determine whether there was evidence of selectivity when crows consumed or cached a walnut. I then performed choice tests to determine which walnut characteristics were preferred by the crows. Finally, I

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provisioned walnuts at a foraging site in order to determine whether crows consumed or cached the types of nuts they had preferred in the choice tests.

MATERIALS AND METHODS

Study Sites and Natural History

I observed crows foraging at English and black walnut trees on Birch Lane (hereafter BL), in Davis, Yolo County, California, U.S.A. In early September crows cached mainly English walnuts that they had removed from trees by prying them loose from their soft outer husk (walnut terminology follows Cronquist 1981). Later, crows cached both black and English walnuts that had fallen to the ground and naturally lost their husks. Walnuts that were not cached were eaten after being opened by repeated dropping on hard surfaces, including asphalt streets near foraging sites and hard-packed soil in agricultural fields at least 1 km away.

By mid-November, all walnuts had fallen from the trees and had been removed by birds, squirrels and humans. I established a new study site 4 km away on the campus of the University of California (hereafter UC) where the crows had previously been attracted to 10 black walnut trees present at this site. I provisioned the site with walnuts that had been gathered at BL and nearby sites. The UC site included parking lots, buildings, lawns and weedy lots. Crows generally cached nuts within 150 m of the provisioning site so transport time was almost negligible during caching. In contrast, at BL, crows often flew several kilometers to cache nuts. Both caching and dropping of walnuts continued for as long as I provisioned nuts. I terminated the study on the first spring morning that I observed crows acting territorially at the provisioning site. All observations were made between 0700 and 1230 hours Pacific Standard Time as crows did not feed on walnuts in the afternoon.

Determining Whether Crows Cached Nuts Selectively

To determine whether crows foraging on naturally occurring nuts were selective about which to cache or consume I tested the null hypothesis of no difference between nuts that were cached and those that were consumed. From 12 September to 1 November 1995 I obtained a sample of cached nuts by following, usually on bicycle, crows departing with walnuts until they landed in agricultural fields at least 1 km away. Cached nuts were well hidden under a thin layer of dry soil, but were not difficult to unearth because the fields were plowed into uniform rows and I could pinpoint precisely the caching locations using a 15 × spotting scope. I recorded the maximum length and width of each collected nut to 0.01 cm using digital calipers. Because walnuts are approximately egg-shaped, volume was estimated using the equation: $V=0.52(LW^2)$, where L is maximum length, and W is maximum width. To assess the pool from which cached English walnuts were selected, I picked one control nut from a randomly selected source tree at BL, and another collected from the ground below, every time a cached walnut was retrieved from the fields. Control nuts gathered from source trees and the ground below did not differ in mean length, width or mass ($N=39$ pairs, all paired t tests: $t<1.5$, all NS), so I averaged these for analysis. I also collected nuts dropped or eaten at BL in the rare instances when this could be done without scaring off the birds. If at least one half of the shell remained intact I measured these nuts in the same manner assuming maximum width and length did not differ between the halves. I did not use mass of a nut as a variable if I did not know that a nut had just been removed from the tree because rapid weight loss occurred due to drying. Thus, some size comparisons were made using volume, while others were made using mass, as noted below.

Determining Crow Preferences

To determine whether crows preferred certain features when choosing a walnut I tested the null hypothesis that crows would show no preference when presented with a pair of walnuts differing in size, species, or condition of the shell. These three variables were used because they represented real choices faced by crows at this site, and each variable has an important effect on the energetic costs and benefits of the choice. English walnuts have 6% more joules per kilogram of cotyledon (i.e. 'meat') and a 21% greater proportion of cotyledon per gram of intact nut (McCarthy & Matthews 1984), and can be cracked more easily (e.g. black walnuts require 8 × more drops to break when dropped from a height of 6 m, Cristol & Switzer 1999). For intact nuts of either species, larger nuts require somewhat fewer drops than smaller ones (Cristol & Switzer 1999). Cracked nuts can be opened by crows without dropping, so they have much shorter handling times than intact nuts (personal observation).

Nuts were presented as pairs with the members of each pair always differing in one of the relevant variables (i.e. size, species or shell condition). I spaced the nuts 10 cm apart so crows could easily compare the two before choosing one and flying away with it. Each trial consisted of five such pairs, each differing in the same variable, each located 7 m apart and presented simultaneously. I stood 50 m away with a 15 × spotting scope and recorded which member of each pair was removed first and the duration of each test. Variables tested were as follows: (1) two English walnuts, one of which was 10% heavier than the other; (2) two English walnuts, one of which was 25% heavier than the other; (3) two English walnuts matched for mass but differing in whether the shell was cracked or intact; (4) two black walnuts, differing only in whether the shell was cracked or intact; and (5) one English walnut and one black walnut, both intact and of approximately the same mass. I conducted approximately two to nine separate tests every other day from 14 November to 4 December 1996 at the UC site. Between each test I randomly changed nut types, alternated right–left position of the nut types, and moved the location of the test by approximately 20 m to reduce

the effects of nut position, preferred routes of entry or previous experience.

It can be assumed that the same crows only rarely made multiple choices within a trial, and thus data points are largely independent, because crows required approximately 2–15 min to cache or consume a walnut at this site (see below) and all 10 nuts were removed quickly on most trials (trial completion: $\bar{X}=5.3 \pm 4.4$ min). The likelihood of one individual contributing to choice trials on different days was greater, but still probably low because 100–1000 individuals were present simultaneously at the study site during all trials, flocks arrived and departed frequently, and approximately 10 000 crows roosted in the vicinity (P. Gorenzel, personal communication).

Determining What Crows Did With Preferred Nuts

Once I had tested whether crows were selective when caching naturally occurring nuts, and whether they showed preferences when choosing provisioned nuts, I tested the null hypothesis that the size, species or shell condition of a nut had no effect on whether crows cached or consumed it. I also included time of day and risk of theft in the analysis to assess possible confounding factors in the crows' selection process. I provisioned 1–30 nuts to crows nearly daily from 16 January to 11 March 1996 at the UC site. A total of 767 nuts were taken on 36 days, and of these, 533 were known to have been cached, eaten, abandoned or stolen. I removed the fleshy husk from all provisioned nuts because when crows found naturally occurring nuts, the husks were already gone or were quickly removed by the birds (personal observation). I placed nuts on the ground, one at a time, at the centre of a parking lot, and crows usually either consumed the nuts after dropping them repeatedly on the asphalt or transported them to adjacent lawns or weedy lots for caching. I presented nuts at one location, in random order with respect to nut type. As in the experiment described above, birds were unmarked and some certainly made repeat visits, but the location of the study site, immediately adjacent to an enormous roost, ensured that a large number of different birds contributed to the data.

To assess risk of theft I made instantaneous counts of all crows visible at a site and estimated the distance to the nearest crow each time a provisioned nut was taken. The number of crows was divided by distance to the nearest crow as an index of risk of theft. This index has been shown elsewhere to be a very accurate predictor of immediate theft or attempted theft of walnuts (Cristol & Switzer 1999). All caches that I observed were also within view of the crows gathered at the study site, however it is not known whether the presence of more potential observers would lead to higher pilfering of these caches in the same way that it leads to higher rates of immediate theft. I recorded time of day whenever a nut was taken, and for analyses, converted this to number of minutes since first light to correct for the effects of seasonal change in sunrise. I attempted to record the amount of time it took each crow to entirely consume a nut, but it was difficult to observe birds for as long as it took them to completely finish (sometimes >10 min); I instead recorded the last time I observed the bird still eating the nut. Finally, to determine whether crows behaved differently when caching more or less preferred nuts, I recorded the number of seconds taken to hide each nut after the bird had finished transporting it.

Statistical Analyses

I used unpaired, two-tailed t tests on untransformed data unless noted. I evaluated dichotomous choice trials with a sign test using the binomial distribution. To determine which factors influenced the likelihood of crows caching or eating provisioned nuts I used a logistic regression model, with walnut species (English or black), mass, shell condition (cracked or uncracked), time of day and index of risk of theft (log transformed) as potential explanatory variables. I used linear and multiple regression to determine the effects of size, species and risk of theft on time spent hiding a nut.

RESULTS

Selectivity During Caching

Of 146 crows observed foraging in English walnut trees at BL, none cached nuts on site. Most flew with a nut directly to surrounding agricultural fields (73%) where they cached or ate it or lost it to a kleptoparasite (unpublished data). The remaining birds attempted to eat their nuts at BL by dropping them from a height (Cristol & Switzer 1999). Nuts transported 1–2 km to agricultural fields did not differ in volume from those that were present at BL (49 cached or eaten nuts from agricultural fields: $\bar{X} \pm \mathrm{SE}=21.5 \pm 2.4$ cm^3; 49 randomly selected control or eaten nuts from BL: $\bar{X} \pm \mathrm{SE}=22.0 \pm 3.7$ cm^3; unpaired t test: $t_{96}=0.7$, $P=0.46$). However, nuts cached by crows in the agricultural fields had significantly smaller volumes than those dropped by crows at BL for immediate consumption (BL: $\bar{X} \pm \mathrm{SE}=22.9 \pm 3.5$ cm^3, $t_{31}=2.3$, $P=0.03$). Thus, crows were not selective about which nuts were transported to the fields, but they were selective about which nuts they ate on site versus those they cached in the fields.

Preferences in Choice Tests

In paired choice tests crows showed strong preferences. They selected English walnuts over black walnuts (100% of 12 pairs; sign test: $P<0.001$) and cracked over intact nuts of both species (English: 78% of 72 pairs; $P<0.0001$; black: 93% of 43 pairs; $P<0.0001$). They chose intact English walnuts that were 25% heavier (69% of 75 pairs; $P<0.01$), but showed no detectable preference for larger nuts when only a 10% difference existed in mass (53% of 95 pairs; $P=0.68$). Casual observations indicated that many of the nuts chosen were consumed immediately after dropping on asphalt, but the proportion cached or consumed is not known.

Caching Provisioned Nuts

For crows foraging on provisioned nuts at UC, a significant portion of the uncertainty in the likelihood of caching was explained by the variables used in the logistic regression model (likelihood ratio: $\chi^2_5=35.3$, $N=338$ nuts, $P<0.0001$). Type of walnut (black versus English), condition of shell (cracked versus intact) and time of day had the greatest effects on the likelihood of caching, such that black walnuts and intact walnuts were more likely to be cached, and the likelihood of caching increased with the number of minutes since first light (species: $\chi^2_1=6.8$, $P=0.009$, condition: $\chi^2_1=10.1$, $P=0.001$, time: $\chi^2_1=9.9$, $P=0.002$). Risk of theft and nut mass had no effect on the model (theft: $\chi^2_1<0.01$, $P=0.9$, mass: $\chi^2_1=0.5$, $P=0.5$). When the same analysis was carried out only on the large sample of 238 English walnuts (i.e. 100 black walnuts excluded), results were similar, with number of minutes since first light and shell condition having significant effects in the model (time: $\chi^2_1=4.2$, $P=0.04$, condition: $\chi^2_1=7.6$, $P=0.006$), and risk of theft and nut mass having no effects (theft: $\chi^2_1=0.3$, $P=0.6$, mass: $\chi^2_1=0.1$, $P=0.7$).

It took 12 crows a mean ± SE of 303 ± 106 s to eat their walnuts, but this is an underestimate, as only 7 of 22 crows observed consuming walnuts for this length of time had finished them. Assuming all crows finished consuming nuts immediately after observations were terminated, the mean time to consume a nut was 360 ± 157 s ($N=29$), which is still an underestimate, and is significantly longer than it took crows to cache nuts (130 ± 110 s, nonparametric test used because of unequal variances; Wilcoxon two-sample test: $Z=6.87$, $N=136$, $P<0.0001$). Thus, consuming a walnut took considerably longer than caching one at this site, and travel time was negligible because all nuts were cached nearby. Crows spent more time caching each English walnut than they did each black walnut (English: $\bar{X}=154 \pm 118$ s; black: $X=98 \pm 91$ s; unpaired t test: $t_{134}=3.0$, $P=0.004$). Because the cached walnuts differed in mass as well as species, it was necessary to determine how much the mass and species of nut contributed to the variance in caching time. Together, mass and species explained a low but significant portion of the variance in caching time (multiple regression: $r^2=0.09$, $F_{2,132}=6.1$, $P=0.003$). Black walnuts were cached significantly more quickly than English walnuts ($F_{1,132}=8.27$, $P=0.005$), but mass had no significant effect on caching time ($F_{1,132}=0.96$, $P=0.33$). No relationship existed between time spent hiding a nut and the risk of theft at the time the nut was obtained (simple linear regression with risk of theft values log transformed: $r^2<0.0001$, $F_{1,121}<0.0001$, $P=0.98$).

DISCUSSION

When foraging in walnut trees crows were selective about which nuts to cache and which to consume, caching nuts with lower volumes. This selectivity in caching was not simply the result of crows avoiding flying long distances with larger nuts, because nuts transported for all purposes (eating and caching) were not smaller than nuts available and eaten on site. When given choice trials, free-living crows preferred English walnuts over black walnuts, an unsurprising result as English walnuts have higher energy value and are easier to break. Consistent with a preference for greater energy content or shorter handling costs, the crows also preferred heavier nuts, which break more easily and have higher energy value. Consistent with a preference for lower handling costs, the crows preferred cracked over intact nuts. Thus, when presented with a choice, crows displayed clear preferences, and those preferences resulted in selection of nuts that provided more energy and required less energy and time to crack. When presented with nuts varying by size, species and shell condition, crows were more likely to cache the less preferred black and intact walnuts. They were also more likely to cache later in the day. Mass of the nut and risk of theft did not affect their caching behaviour. When they did cache a preferred English walnut, they spent longer hiding it than they did a black walnut, while mass and risk of theft again did not affect time spent hiding.

Do crows cache less preferred nuts because they have greater handling time, as reported for squirrels, shrews and other small mammals (Jacobs 1992; Rychlik 1999 and references therein)? This hypothesis should apply when caching takes less time than consuming and the forager is partially satiated and time limited. Consistent with this explanation, crows were more likely to cache less desirable nuts, and these are the nuts that would have required more time or energy to crack open for immediate consumption (black, and intact walnuts require more drops). Contrary to this explanation, mass of provisioned nuts did not affect the likelihood of caching, despite the fact that lighter nuts require more drops to break. However, somewhat in contrast to this result and consistent with the idea that handling time influences caching behaviour, crows foraging in the walnut grove at BL did select nuts with smaller volume when caching. Therefore, in three of four independent comparisons, crows preferentially cached the types of nuts that would have required greater handling cost to eat (i.e. black and intact provisioned walnuts and unprovisioned walnuts with smaller volumes).

It is interesting to note that mass, the one variable not conforming to the handling cost explanation, also did not have the predicted effect on dropping behaviour of crows (Cristol & Switzer 1999). There are several possible explanations. Crows may not be able to assess mass as accurately as other variables (but see Langen & Gibson 1998). This is consistent with the result that despite a preference for walnuts that were 25% heavier, the crows showed no preference for nuts that were 10% heavier; perhaps they were unable to detect 10% differences in mass. Alternatively, mass, which is only a weakly significant predictor of breakability (Cristol & Switzer 1999), may be ignored by crows. Unfortunately, the data in this study do not allow further speculation because, due to time constraints, the volume of provisioned nuts was not measured, and the mass of cached nuts could not be used because of uncertainty as to how long they had been drying off the tree before being cached.

The hypothesis that crow preferences and caching behaviour are influenced by handling costs is consistent

with my results, but alternative explanations exist for some of the results. Because English walnuts have higher energy value as well as lower handling requirements, it is not possible to distinguish energy value from handling time without further experiments in which the two are dissociated. The greater likelihood of caching intact nuts, which have the same energy value as cracked nuts but greater handling time, would implicate handling costs as the variable crows were using, except that a different alternative explanation exists for this behaviour. Intact nuts are less perishable than cracked nuts, and perishability is used by some animals in making caching decisions (e.g. Hadj-Chikh et al. 1996).

The crows' caching behaviour contrasts with that of nuthatches, which cache preferred sunflower seeds from which husks have been removed (by a researcher), but consume immediately those seeds that require time-consuming husk removal (Woodrey 1990). The nuthatches' behaviour was explained as being the result of the birds maximizing the value of each food item by caching for security against starvation later in the day. Since pilferage rates were assumed to be low in territorial nuthatches, caching the more valuable items and leaving less valuable ones to an uncertain fate on the feeder may have increased overall daily energy gain. The caching of less preferred items by squirrels in the laboratory (Jacobs 1992), which has also been reported for other rodents (e.g. Ivan & Swihart 2000), may be the result of adaptations for longer-term hoarding or greater pilferage rates, both of which would reduce the likelihood of retrieval. In the present study crows were faced with the option of investing a lot of time to consume a walnut immediately, or less time to cache it for later use. Paradoxically, if an item is cached, more time will be required to consume it at some later date and the overall investment in that item will be greater than if the item had been consumed immediately. Perhaps natural selection has favoured those crows that place less preferred items in caches because these birds then spend more time consuming preferred items, retrieving their less preferred items only when starving or when not time limited. Experimental studies in which cache duration and pilferage rates can be controlled will be necessary to determine whether an animal's tendency to cache or eat preferred items responds to certainty of retrieval.

Crows spent more time choosing and preparing a cache for each English walnut than each less preferred black walnut. If it is assumed that increased time spent choosing a location and carefully burying an item lower the risk of pilfering, then it makes sense for crows to invest more when caching more valuable food items, such as English over black walnuts. (By way of comparison, the crows in this study spent four times longer storing each item than was spent by territorial crows described in Verbeek (1997).) Like these walnut-caching crows, nuthatches spend more time hiding more valuable sunflower seeds from which they have previously removed the hulls (Moreno & Carrascal 1995). Several other bird species invest more time in more valuable food items because they carry them farther from food sources before storing them, as predicted by optimality models based on minimization of pilfering (e.g. Jokinen & Suhonen 1995). Squirrels cache walnuts farther from a feeder during the time of year when pilfering rates are highest (Tamura et al. 1999), and several other mammals also cache more valuable items farther from food sources (e.g. Vander Wall 1995). Crows showed the same increased investment of time in more valuable caches as found in many other species, however, the increased investment was spent in more carefully choosing the cache site and/or covering the item, rather than transporting the food farther from the food source. It should not be assumed, in future tests of optimal cache distribution models, that when animals spend more time making a cache that they have necessarily travelled farther.

Time of day, or more specifically, number of minutes since first light, was another good predictor of caching behaviour. Time of day may have affected likelihood of caching indirectly because it is a correlate of satiety. The longer a bird has been active, the less likely it is to need to consume food immediately to meet its daily energy needs. Alternatively, time of day may play a role in a bird's strategic decisions with regard to managing risk of starvation. Time of day has previously been reported to affect caching behaviour in some small birds (references in Lahti & Rytkönen 1996) but not others (Brotons 2000). Until cache duration for walnuts cached by crows is known it will not be possible to evaluate the roles of satiety and risk management in the walnut-caching behaviour of crows.

To summarize, in choice tests crows preferred nuts with shorter handling times (i.e. heavier, English and cracked walnuts). They were more likely to cache less preferred varieties of nuts (i.e. smaller volume, black and intact walnuts). The hypothesis that crows cache nuts with longer handling times and eat immediately those with shorter handling times is the most parsimonious explanation of these results. Because two of the three varieties of nuts that crows preferred to consume immediately had higher energy contents (heavier and English walnuts), and at least one of the three varieties that crows tended to cache was less perishable (intact walnuts), energy content or perishability could also explain some of the results, but an explanation based on handling time predicted the most findings.

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