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Avian prey-dropping behavior. II. American crows and walnuts

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Complex and energetically expensive foraging tasks should be shaped by natural selection to be efficient. Many species of birds open hard-shelled prey by dropping the prey repeatedly onto the ground from considerable heights. Urban-dwelling American crows (*Corvus brachyrhynchos*) forage in this way on two species of walnuts in central California, USA. As predicted from a theoretical model, crows dropped nuts with harder shells from greater heights and dropped them from greater heights when over softer substrates. The height selected for dropping nuts decreased in the presence of numerous nearby conspecifics, indicating that crows were sensitive to the risk of kleptoparasitism when selecting drop heights. Drop height decreased with repeated drops of the same walnut, suggesting that crows adjusted for the increasing likelihood that a repeatedly-dropped nut would break on subsequent drops. Crows did not alter height of drop in accordance with differences in the mass of the prey. When faced with multiple prey types and dropping substrates, and high rates of attempted kleptoparasitism, crows adjusted the height from which they dropped nuts in ways that decreased the likelihood of kleptoparasitism and increased the energy obtained from each nut. *Key words:* American crow, *Corvus brachyrhynchos*, foraging behavior, *Juglans* spp., kleptoparasitism, prey dropping, walnuts. *[Behav Ecol 10:220–226 (1999)]*

Birds that break open hard-shelled prey items by dropping them repeatedly onto the ground have attracted scientific attention for at least a century (e.g., Saunders, 1891). This foraging behavior is more complex than most because it requires repeated flights with a prey item, choice of drop sites and drop heights, and retrieval of prey. Such a demanding task is ideal for studying how closely an animal's behaviors are adapted to the rigors of its environment. Because avian prey-dropping occurs in at least three distantly-related orders of birds (Table 1), this behavior has presumably evolved a number of times. The occurrence of avian prey-dropping on nearly every continent, in a wide-range of habitats, and with many different types of prey suggests the potential for interesting adaptive modifications (Table 1). Finally, the occurrence of prey dropping among both highly gregarious and essentially solitary species raises the question of whether, when, and how this complex behavior is learned.

Much of the early interest in avian prey-dropping behavior arose from debate over whether some birds (crows) selected efficient hard surfaces for dropping, whereas others (gulls) were less "intelligent" because they reportedly failed to discriminate between hard and soft substrates (Oldham, 1930; Tinbergen, 1960). More recently authors have attempted to understand avian prey-dropping in the context of optimal foraging (e.g., Barash et al., 1975; Beck, 1980; Maron, 1982; Siegfried, 1977; Whiteley et al., 1990; Zach, 1978, 1979). In our companion paper (Switzer and Cristol, 1999) we presented a general theoretical model that identifies important variables that should shape all avian prey-dropping systems. The model suggests that the height from which hard-shelled prey will be dropped is influenced by the hardness of the prey item, the hardness of the substrate onto which it is dropped, the mass of the prey item, the potential weakening of the shell during repeated drops, and the likelihood of loss after dropping. The objective of the present study was to test the qualitative predictions of our model on a previously undescribed avian prey-dropping system.

American crows, *Corvus brachyrhynchos*, which drop two species of walnuts (English, *Juglans regia*, and northern California black, *J. hindsii*), presented an ideal opportunity to test our model. We first gathered background data on the heights from which we had to drop each type of walnut until it was cracked sufficiently to be consumed by a crow and data on the effects of different substrates, nut mass, and repeated impacts on the breakability of the walnuts we dropped. We also determined, by observing foraging crows, whether the probability of a crow losing its walnut was dependent on the height from which the nut was dropped. These data allowed us to choose a specific set of predictions from our general theoretical model that could be applied to the crow–walnut system (Switzer and Cristol, 1999). To test these predictions we gathered data on the heights from which crows dropped walnuts in situations where important factors could be varied. For example, we observed crows feeding simultaneously on two walnut species that differed markedly in the ease with which they could be broken, thereby allowing us to test predictions about the effects of prey hardness on the height selected for dropping.

A central prediction of our model was that the presence of prey loss should have dramatic consequences on dropping behavior (Switzer and Cristol, 1999). Although prey loss and theft are mentioned in most previous studies of prey dropping (e.g., Barash et al., 1975; Siegfried, 1977; Whiteley et al., 1990; Zach, 1979) few quantitative data are available. In the present study, crows frequently stole walnuts dropped by other crows, and dropping occurred under varying degrees of kleptoparasitism intensity. Thus, we were able to examine, for the first time, the effects of prey loss on this complex foraging behavior.

CHARACTERIZING WALNUTS

Methods

Before making specific predictions using the model presented in our companion paper, it was necessary to understand the effects of height, prey type, substrate hardness, repeated drops, and prey mass on the probability of a prey item break-

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Table 1

Bird species and the prey they drop

Bird species	Prey types (no. of reported prey species)	Reference
Corvus brachyrhynchos (American crow)	Nuts (3)	Switzer and Cristol, 1999; Grobecker and Pietsch, 1978; Maple, 1974
C. caurinus (northwestern crow)	mollusks (3)	James and Verbeek, 1984; Richardson and Verbeek, 1986, 1987; Zach, 1978
C. corone cornix (hooded crow)	Mollusks (4), nuts (3), crustaceans	Berrow et al., 1992; Förstel, 1993; Lorek and Oleksik, 1992; Mienis, 1993
C. c. corone (carrion crow)	Mollusks (2), nuts (2)	Nihei, 1995; Oldham, 1930; Saunders, 1891; Tinbergen, 1960; Whiteley et al., 1990
C. frugilegus (rook)	Mollusks	Priestley, 1947
C. monedula (jackdaw)	Nuts	Gibson, 1992
C. moneduloides (New Caledonian crow)	Nuts	Hunt, 1996
C. corax (common raven)	Mollusks, bones	Heinrich, 1989; van Lawick-Goodall, 1970
C. albicollis (white-necked raven)	Turtles	Uys, 1966, cited in Goodwin, 1986
Gypaetus barbatus (lammergeier)	Bones, turtles	Hartley, 1967; Huxley and Nicholson, 1963
Neophron percnopterus (Egyptian vulture)	Turtles	Lesham, 1979, cited in Boswall, 1983
Pandion haliaetus (osprey)	Mollusks	Lesham, 1979, cited in Boswall, 1983
Haliaetus leucocephalus (bald eagle)	Turtles	Bindner, 1968
Aquila chrysaetos (golden eagle)	Turtles	citations in Boswall, 1983
Catharcta skua (South polar skua)	Eggs	Sladen, 1958, cited in Boswall, 1977
Larus argentatus (herring gull)	Mollusks (8), fish, crustaceans (4), echinoderms (2)	Beck, 1980; Cadée, 1989; Cavanagh, 1992; Connor, 1993; Ingolfsson and Estrella, 1978; Kent, 1981; Oldham, 1930; Tinbergen, 1960
L. delawarensis (ring-billed gull)	Mollusks (3)	Drennen, 1995
L. canus (mew gull)	Mollusks	Oldham, 1930
L. dominicanus (kelp gull)	Mollusks (>2)	Siegfried, 1977; Ward, 1991
L. glaucescens (glaucous-winged gull)	Mollusks (2)	Barash et al., 1975
L. marinus (great black-backed gull)	Mammals, eggs	Harber and Johns, 1947; Tinbergen, 1960
L. melanocephalus (Mediterranean gull)	Mollusks (2)	van Impe, 1978
L. occidentalis (western gull)	Mollusks (5)	Maron, 1982
L. pacificus (Pacific gull)	Mollusks (2), echinoderms	Teichert and Serventy, 1947; Wheeler, 1946

ing open on a given drop (Switzer and Cristol, 1999). We determined these characteristics for walnuts by dropping them from an exterior stairway at various heights.

To determine the effect of height on the probability of a dropped walnut breaking, we dropped 20 English walnuts onto asphalt at each of the following heights: 1.55, 3.1, 6.2, and 9.3 m. Each nut was dropped repeatedly from the same height until its shell had cracked open sufficiently to be consumed by a crow (throughout the paper "cracked" refers to a hole of at least 1 cm^2). The same procedure was repeated with black walnuts from 3.1, 6.2, and 9.3 m. A two-factor (species, height) ANOVA was used to compare the number of drops required to break English and black walnuts dropped from these three heights.

To determine the effect of substrate hardness on the probability of a dropped walnut breaking, English walnuts were dropped from 6.2 m and 9.3 m into a container of hard-packed soil from an agricultural field used by crows for nut dropping. These were compared with English walnuts dropped from the same heights onto asphalt. Nuts that had not broken after 20 drops were assigned a value as if they had broken on the next drop. We used a nonparametric Mann-Whitney *U* test to compare the breakability of all English walnuts dropped on each of the two substrates because variance was distorted by the fact that all nuts dropped on soil from 6.2 m were scored as having broken after 21 drops.

To determine whether walnuts weakened with repeated drops, 100 English walnuts weighing from 6–17 g were dropped repeatedly from 3.1 m until cracked. So that we could compare our results to those of a previous study on dropped mollusks (Zach, 1979), we plotted the percentage of nuts broken in each batch of redropped nuts. With arcsine-transformed data from our walnuts and Zach's mollusks (1979), we used linear regression to determine whether either relationship was positive. A positive slope would indicate weakening with successive drops. This was repeated for 100 black walnuts of similar weights dropped from 10.85 m, which is a comparable height in terms of the number of drops required to crack these harder nuts. Black walnuts exhibited a similar pattern to English walnuts (data not shown), but because we have insufficient data to examine the behavior of crows successively dropping black walnuts (see below), there was no reason to include black walnuts in this analysis. The same black and English walnut data were used to determine the relationship between number of experimental drops required to break a walnut and its mass.

Results

By dropping nuts experimentally, we found that the number of drops required to crack a walnut decreased with height of drop, regardless of species ($F_{\text{height}} = 27.7$, df = 2, $p < .0001$; Figure 1). English walnuts broke more easily than black walnuts, regardless of height ($F_{\text{species}} = 119.8$, df = 1, $p < .0001$; Figure 1). There was also a significant interaction between species and height ($F_{\text{interaction}} = 19.7$, df = 2, $p < .0001$), reflecting the fact that further increases in height, beyond the height at which all were broken, could have no effect on the likelihood of an English walnut breaking. Thus, walnuts are more likely to break when dropped from higher heights, and black walnuts require more drops to break than do English walnuts.

English walnuts dropped experimentally onto asphalt broke in fewer drops than those dropped onto soil (asphalt: $n = 40$ walnuts, mean $= 1.3 \pm 0.5$ drops; soil: $n = 40$ walnuts, mean $= 13.9 \pm 7.6$ drops; $z = 7.2$, $p < .0001$; Figure 1), indicating

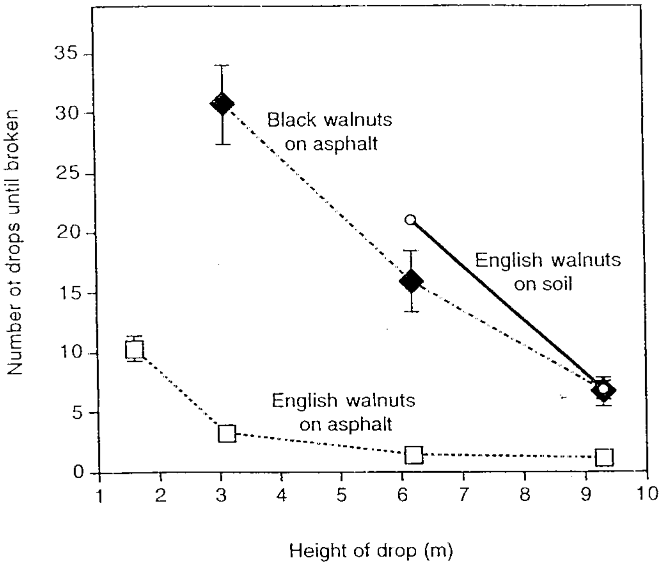

Figure 1
Number of drops required to break English (open symbols) and black (filled symbols) walnuts from various heights on asphalt or soil. The figure shows that both species of walnuts break more easily when dropped from greater heights, English walnuts are easier to break than black walnuts, and English walnuts break more easily on asphalt than soil. Each symbol represents the mean (± SE) of 20 walnuts. (SE not shown when smaller than height of symbol.)

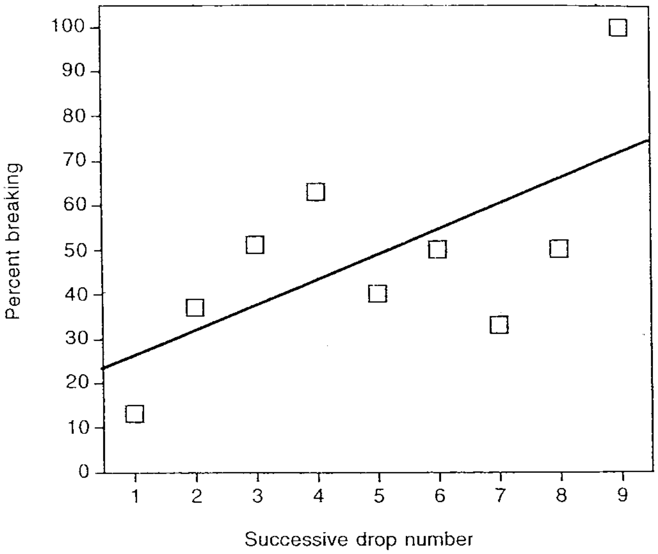

Figure 2
The probability of an English walnut breaking tended to increase after repeated drops ($y = 0.20 + 0.06x$, $r^2 = .42$, df = 7, $F = 5.2$, $p = .056$). Similar data for mollusks indicate that they do not become more likely to break after repeated drops ($y = 0.28 - 0.005x$, $r^2 = .01$, df = 7, $F = 0.7$, $p = .43$; see Zach, 1979, for data).

that asphalt is a more effective substrate for breaking nuts than agricultural soil.

English walnuts tended to be more likely to break after repeated drops (Figure 2). By way of comparison, the mollusks studied by Zach (1979) did not become increasingly likely to break after repeated drops.

The relationship between mass and the number of drops required to break English and black walnuts was weakly but significantly negative (English: $y = -0.2x - 5.2$, $r^2 = .10$, df $= 78$, $F = 8.7$, $p = .004$; black: $y = -1.0x + 15.5$, $r^2 = .419$, df $= 96$, $F = 22.3$, $p < .0001$). In other words, heavier nuts were slightly easier to break, but large sample sizes were required to detect the effect.

STUDY SITES AND GENERAL METHODS

We observed crows foraging on nuts in English and black walnut trees in urban areas of Davis, Yolo County, California, USA. From 12 September to 1 November, 1995 crows were observed almost daily at our primary location, Birch Lane, a low-traffic residential street with 25 English walnut trees. Occasionally we observed crows dropping English walnuts from Birch Lane onto the dried soil of nearby agricultural fields. We also observed crows dropping black walnuts 3–9 January 1996 at a second site, Russell Boulevard, a high-traffic road located 5 km from Birch Lane with approximately 100 large black walnut trees.

All English walnuts had fallen from the trees and been removed by birds, squirrels, and humans by mid-November, and all black walnuts were gone by mid-January. Therefore, we established a new study site, on the campus of University of California-Davis, where we provisioned free-living crows with walnuts nearly daily from 16 January to 11 March 1996. Our objective at the campus site was to determine experimentally the drop heights of English and black walnuts of known mass (to 0.1 g) dropped at the same site under identical conditions.

We recorded the following data for each instance of a crow dropping an English walnut at Birch Lane: height (estimated by comparison with previously measured trees, utility poles, and other objects); distance each nut rolled; number of times each nut was dropped; number of crows present within 100 m; ground distance from where the crow dropped the nut to the nearest other crow; and response of other crows (kleptoparasitize, attempt to kleptoparasitize, or no response, all within 30 s). In nearby agricultural fields, and at Russell Boulevard, we recorded only the heights from which walnuts were dropped and the number of drops for each nut. At the campus site walnuts were presented singly or in pairs, and each crow taking a provisioned walnut was followed until the nut was either eaten or stolen or until the bird disappeared from view.

All provisioned walnuts were gathered in October 1995 from single trees of each species, except for English walnuts >17.5 g, which were gathered from a different tree. At Birch Lane and Russell Boulevard crows found naturally occurring nuts and removed the soft hulls before dropping, whereas at the campus site all nuts were provisioned with hulls already removed. Throughout the study all observations were made during the first 4 h after dawn. Crows were unmarked, but the rapid turnover of flocks and large number of individuals present simultaneously at the study sites (100–1000 individuals daily), the large number of crows roosting in the vicinity (approximately 10,000; Gorenzel P, personal communication), and an analysis of the variability in dropping behavior of 21 recognizable individuals (Cristol and Switzer, unpublished data; see Leger and Didrichsons, 1994) indicate that our conclusions are robust despite the occasional inclusion of some multiple observations from the same individuals. Except when considering the effects of repeated drops, all data were from the first-time drops only. Throughout, unpaired *t* tests, simple linear regression, and ANOVA were used unless otherwise noted.

CHARACTERIZING PREY LOSS

Methods

An essential characteristic of any avian prey-dropping system is the likelihood of losing prey before it can be retrieved, such as through kleptoparasitism. Prey loss, if it occurs, might be constant with regard to drop height, or it might increase when a bird drops prey from greater heights. We examined our data from crows feeding on naturally occurring English walnuts at Birch Lane to determine both the prevalence of walnut loss in this system and whether the probability of loss through kleptoparasitism was dependent on height of drop. To determine whether height of drop affected the likelihood of kleptoparasitism, we used logistic regression (SAS JMP 3.1) with "kleptoparasitized" or "not kleptoparasitized" as the dependent variable, and drop height, distance to nearest crow, number of crows present, and distance the nut rolled as independent variables. Because attempted kleptoparasitism was much more frequent than actual kleptoparasitism, we performed an alternative analysis with "attempted kleptoparasitism" as the dependent variable.

Results

Prey loss occurred almost exclusively through kleptoparasitism (data not shown), with nearly half of all first-time drops resulting in attempted kleptoparasitism, and 12% of all dropped nuts being stolen. A significant portion of the uncertainty in likelihood of kleptoparasitism was explained by the factors included in our logistic regression model (df = 4, likelihood ratio $\chi^2 = 20.2$, $p < .0005$). Height from which a walnut was dropped had the greatest effect on the model (df = 1, Wald $\chi^2 = 6.9$, $p = .009$). Our alternative logistic regression model explained more of the uncertainty in the likelihood of attempted kleptoparasitism (df = 4, likelihood ratio $\chi^2 = 58.9$, $p < .0001$), and the drop height again had the greatest effect on the model (df = 1, Wald $\chi^2 = 7.3$, $p = .007$). Thus, the likelihood of prey loss through kleptoparasitism was related to the height of drop for English walnuts.

TESTING PREDICTIONS OF THE MODEL

Having determined the relevant prey characteristics and details of kleptoparasitism for this previously undescribed avian prey-dropping system, we tested five key predictions generated by our model (Switzer and Cristol, 1999).

Prediction 1: prey breakability

Because English walnuts break more easily than black walnuts, crows should drop English walnuts from less high than they do black walnuts.

Methods. We compared the heights from which crows dropped each walnut species when they were foraging on naturally occurring English walnuts at Birch Lane and black walnuts at Russell Boulevard. We also compared drops of the same two nut species when they were provisioned simultaneously at the campus site where birds dropped them under identical conditions.

Results. The mean height for 311 first-time drops at Birch Lane was 3.41 ± 2.17 m, with a maximum recorded drop of 10.85 m. Crows dropping black walnuts at Russell Boulevard dropped them from significantly greater heights than crows dropping English walnuts at Birch Lane ($n = 34$, mean = 7.01 ± 3.18, df = 343, $t = 5.7$, $p < .0001$). Where both walnut species were dropped together, at the campus site, crows also dropped the black walnuts from significantly greater heights than they did English walnuts (English: $n = 153$, = 4.66 ± 3.02 m; black: $n = 72$, = 5.84 ± 3.15 m, df = 223, $t = 2.7$, $p = .0075$). Because English walnuts varied in mass more than black walnuts, we also compared drop height for only those English walnuts within the range of weights represented by black walnuts (6.7–13.7 g) and found a similar result (English: $n = 95$, = 4.83 ± 3.48 m; df = 165, $t = 2.3$, $p = .02$). Crows dropped the harder-to-break black walnuts from greater heights than they did English walnuts, supporting this prediction of our model.

Prediction 2: substrate hardness

Because English walnuts break more easily on asphalt than on soil, crows should drop them from greater heights when they are over soil. As a corollary to this prediction, crows should select paved surfaces in preference to soil when both are available.

Methods. We compared heights from which crows dropped naturally occurring English walnuts on paved surfaces at Birch Lane and on agricultural fields nearby. To determine whether crows preferentially dropped English walnuts onto hard surfaces when both paved and softer substrates were available, we observed an area of 771 m^2 at Birch Lane and recorded the surface onto which the first 50 walnuts were dropped by crows. The measured site was 41.7% asphalt, 20.0% concrete, and 38.3% lawn. We recorded only the first drop for each nut.

Results. Crows that dropped walnuts onto the soil of agricultural fields did so from significantly greater heights than those dropping onto the asphalt or concrete of Birch Lane ($n = 36$, mean = 8.47 ± 6.72 m, df = 345, $t = 9.5$, $p < .0001$). When dropping in an area where we had measured substrate availability, crows dropped 48 English walnuts onto asphalt or concrete and only 2 onto lawn during our observations ($\chi^2 = 24.8$, $p = .001$, df = 1). As predicted, crows dropped walnuts from greater heights on the softer substrate and selected paved surfaces as dropping substrates significantly more often than expected by chance.

Prediction 3: height of successive drops

Because the probability of a walnut breaking increases with each additional drop, crows should reduce the height of successive drops of the same nut.

Methods. To determine whether height of drop changed during series of repeated drops, we compared mean heights of first, second, third, fourth, and all other drops combined (fifth through seventeenth). Because our independent variable is not on an interval scale, we used a nonparametric Kruskal-Wallis test with multiple comparisons (Siegel and Castellan, 1988). To determine whether any relationship between drop height and successive drop number might be affected by a third variable, attempted kleptoparasitism, we also compared the percentage of first, second, third, fourth, and all other drops that resulted in attempted kleptoparasitism using the same statistical test described above.

Results. At Birch Lane 11.9% of 337 English walnuts dropped once were dropped again by the same crow (mean = 3.42 ± 1.87 drops). The maximum number of repeated drops observed at Birch Lane was 17, although at other sites crows dropped English walnuts up to 50 times before cracking them (data not shown). As predicted by our model, drop height decreased significantly with successive drops (Figure 3). Attempted kleptoparasitism did not change with successive drops (df = 4, Kruskal-Wallis $H = 4.0$, $p = .41$), indicating that this variable is unlikely to explain the relationship between drop height and successive drop number.

Prediction 4: prey mass and breakability

Because heavy walnuts break more easily than light ones, crows should drop heavier walnuts from lower heights than lighter ones.

Methods. Using data from the provisioned walnuts of known mass dropped at the campus site, we determined whether

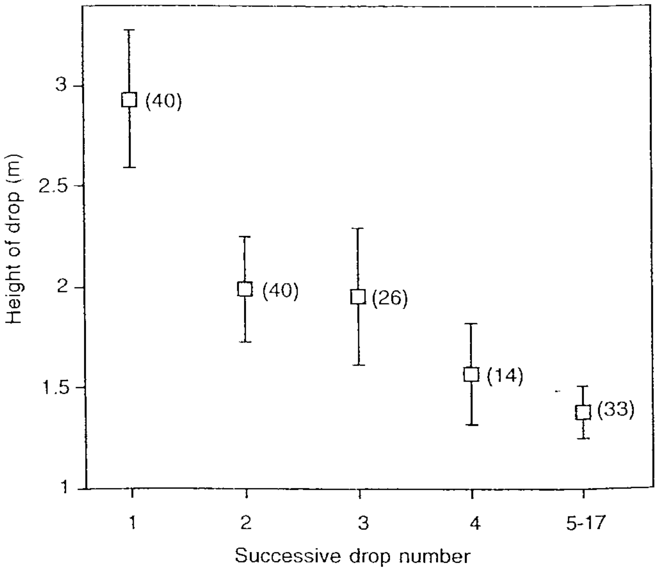

Figure 3
Mean (± SE) height to which crows carried English walnuts on successive drops. Walnuts were dropped from lower heights on successive drops (df = 4, Kruskal-Wallis $H = 13.5$, $p = .008$), but multiple comparisons indicated that none of the differences between particular successive drops was significant alone (all difference in ranks < 24.05, all $p > .05$). Numbers of drops in parentheses.

there was a significant relationship between nut mass and height of drop using linear regression.

Results. Contrary to our prediction, there was no relationship between mass and drop height for provisioned English walnuts ($y = 11.38 + 0.28x$, $r^2 < .01$, df = 151, $F = 1.0$, $p = .32$). Further, heavy black walnuts were dropped from significantly greater heights than light ones, although mass explained only a small percentage of the variation in drop height ($y = -0.65 + 1.81x$, $r^2 < .08$, df = 70, $F = 5.6$, $p = .02$). Thus, crows did not drop heavier walnuts from lower heights, failing to support the prediction of the model.

Prediction 5: prey loss

Because the probability of prey loss through kleptoparasitism by other crows increases with drop height, crows should decrease drop height when there is a greater risk of kleptoparasitism.

Methods. To determine whether crows adjusted drop height with respect to potential kleptoparasitism, we tested for a correlation between drop height and an index of "kleptoparasite intensity," using the data from all first drops of English walnuts at the Birch Lane site. Our index of kleptoparasite intensity was the number of crows present divided by the distance to the nearest crow. We do not know what measure crows might use in assessing risk of kleptoparasitism, and complicating factors such as social status could make assessment difficult. In the absence of such information, we used a simple index because it combined the two pieces of information that we, and presumably the crows, could easily measure during the rapid-paced events of a walnut drop. Our index of kleptoparasite intensity proved to be an excellent predictor of the probability of kleptoparasitism and/or attempted kleptoparasitism. To determine this we classified each drop as being one of eight ordinal categories of increasing kleptoparasite intensity (levels chosen to equalize sample sizes in each category), and then we performed a nonparametric test of association between this index and the observed levels of kleptoparasitism and/or attempted kleptoparasitism (Spearman $\rho = 0.98$, $p = .01$).

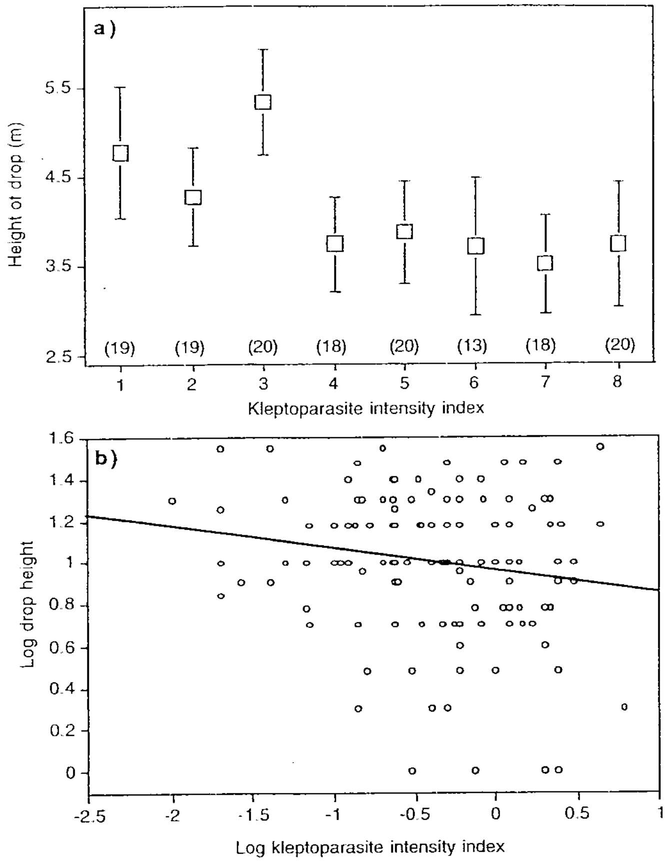

Figure 4
Crows dropped English walnuts from greater heights when kleptoparasite intensity index (number of crows/distance to nearest crow) was lower. (a) Correlation between the kleptoparasite intensity index and mean (±SE) height of drop (Spearman $\rho = -0.83$, $p = .03$). Sample sizes shown in parentheses (see text for description of index categories). (b) Regression of log-transformed data ($y = 0.95 - 0.12x$, $r^2 = .04$, df = 135, $F = 6.2$, $p = .01$).

We used two alternative analyses to determine whether drop height was related to risk of kleptoparasitism: (1) we carried out a nonparametric test of association between the index of kleptoparasite intensity and height of each drop, and (2) we used linear regression after log transforming both the drop height and kleptoparasitism intensity index data so that they closely approximated normal distributions.

Results. As predicted, there was a significant negative relationship between drop height and kleptoparasite intensity, indicating that crows dropped walnuts from greater heights when the potential for kleptoparasitism was lower. Both the nonparametric analysis on the untransformed data (Figure 4a) and linear regression on log-transformed data indicated significant relationships (Figure 4b).

DISCUSSION

Prey breakability

Our model predicted that birds should drop harder-to-break prey from greater heights, a prediction best tested with a single species that drops multiple prey types. Crows chose significantly greater heights when dropping black walnuts, which are harder than English walnuts. This is the first demonstration that birds adjust drop height according to hardness of prey and was true for naturally occurring English and black walnuts dropped at separate sites and for experimental data from provisioned walnuts dropped simultaneously at a single site.

Substrate hardness

For the same reason that birds should drop harder prey from greater heights, our model predicted that they should drop prey from lower heights when they are over harder substrates. When dropping English walnuts onto harder, paved surfaces crows dropped prey from lower heights than when dropping the same walnuts over the softer substrate of nearby agricultural fields. Thus, as predicted by our model, crows adjusted the height of their drops according to substrate hardness, consistent with earlier reports of crows and gulls dropping mollusks on different substrates (Siegfried, 1977; Ward, 1991; Whiteley et al., 1990)

Numerous reports of birds selecting distant or traditional drop sites, such as ossuaries used by lammeregeiers (*Gypaetus barbatus*; Huxley and Nicholson, 1963), are highly suggestive of substrate selectivity by most prey-dropping birds, but the issue of substrate selectivity has not been satisfactorily resolved because researchers have consistently failed to report the available area of each type of substrate (e.g., Barash et al., 1975; Beck, 1980). At a site where we had measured relative substrate availability, American crows selected paved areas as drop sites significantly more frequently than if they had been dropping without regard to substrate. Whether there is great variability between species in the ability to select effective dropping substrates, as suggested by Tinbergen (1960), remains to be determined from comparative studies in which substrate availability is quantified.

Height of successive drops

Our model predicted that a foraging bird should adjust drop height according to the probability that the prey item will break on that drop. Some prey items, such as certain mollusk species, have the same chance of breaking regardless of how many times they have been dropped. Crows dropping those mollusks have been reported to drop them from constant or slightly increasing heights on successive drops (Whiteley et al., 1990; Zach, 1978). By dropping English walnuts repeatedly until they broke, we demonstrated experimentally that, in contrast to many mollusks, walnuts have an increasing probability of breaking with repeated impacts. As predicted by the model, American crows dropped English walnuts from lower heights on successive drops. Thus, our model successfully predicted a behavioral difference between two avian prey-dropping systems based on a specific characteristic of the prey—change in breakability on successive drops.

Prey mass and breakability

For cases in which prey breakability reliably increases with prey weight, our model predicted that birds would adjust drop height and drop harder-to-break prey from greater heights. For both species of walnuts there was a significant but weak positive relationship between prey mass and breakability. Because heavier walnuts break more easily crows should drop them from lower heights than lighter walnuts. Crows apparently adjusted height of drop according to prey mass when dropping black, but not English, walnuts. However, heavier black walnuts, which break more easily, were dropped from greater heights than light ones, opposite of what was predicted by our model. This lack of support for the model's prediction could be the result of crows ignoring walnut mass because it is a poor predictor of breakability or crows failing to accurately assess walnut mass. Another possibility is that crows chose greater drop heights for heavier black walnuts because the greater energetic value of the larger nuts outweighed the potential energetic savings resulting from their slightly greater breakability (Switzer and Cristol, 1999). Little is known about the ability of corvids to assess prey mass per se, so without further study we cannot distinguish between these explanations (references in Vander Wall, 1990).

Prey loss

Little attention has been paid to the role of prey loss in avian prey-dropping systems. Given that kleptoparasitism was the main form of prey loss for American crows dropping walnuts and that its likelihood increased with drop height, our model predicted that drop height should increase when potential kleptoparasitism was lower. Using an index that combined the number and proximity of conspecifics, we showed that crows dropped walnuts from greater heights as the likelihood of kleptoparasitism decreased, supporting a key prediction of the model. Although the negative relationship between drop height and kleptoparasitism risk was significant, the nonparametric analysis shown in Figure 4a suggests that there may be a threshold of kleptoparasite intensity above which drop height is reduced, rather than the linear response suggested by the parametric analysis (illustrated in Figure 4b). Further work is necessary to uncover the means by which crows assess risk of kleptoparasitism and to reveal the details of their behavioral response.

Kleptoparasitism is of varying importance in other avian-prey dropping systems. It is apparently unimportant for territorial northwestern crows dropping whelks (Zach, 1978), while other studies mention that theft occurs (e.g., Siegfried, 1977), or even suggest the possibility of territorial defense of drop sites against kleptoparasites (Barash et al., 1975). Only one previous study has presented any data addressing this question. Whiteley et al. (1990) found that the average height from which mussels were dropped when there were more than five crows and/or gulls within 8 m of a dropping crow was 52% lower than the height used when no potential kleptoparasites were present, but no other data on kleptoparasitism were reported. There are other data in the literature suggesting that birds adjust drop height to account for probability of kleptoparasitism, but they have not been interpreted in this light by the authors. Gulls tended to drop prey from approximately 60% lower heights when at a more crowded site, but Siegfried (1977) attributed this to the fact that the more crowded site had a harder substrate. Beck (1980) reported that the mean drop height for gulls using a rock wall with many other gulls was 34% lower than that for a parking lot with fewer gulls, but his explanation was that the narrow wall required better aim. Many studies mention kleptoparasitism and other forms of prey loss (e.g., lost under water or lost among broken shells), but ours is the first in which the likelihood of prey loss and its relationship with drop height has been quantified.

Conclusions

American crows foraging on walnuts presented an opportunity to test our model of prey-dropping behavior on a previously undescribed system. Because crows dropped two species of walnuts that differed substantially in hardness, and they dropped prey onto both paved and unpaved substrates, we had the opportunity to test several predictions of our model within the same avian prey-dropping system. Because birds drop many types of hard-shelled prey (Table 1), the present study also allowed us to compare the crow–walnut system to other examples of avian prey-dropping. Walnuts differ from commonly dropped mollusks in two ways that affect the predictions of our model: walnuts are more likely to break with each successive drop, and heavier walnuts break more easily than lighter ones.

Our model predicted that if birds maximize the energy obtained from each dropped food item, they should take into account the intensity of kleptoparasitism, the likelihood of each item breaking given its hardness and previous weakening, and the hardness of the substrate. American crows adjusted the height from which they dropped walnuts as our model predicted, if they were accounting for each of these factors. Crows did not behave as predicted with regard to the mass of a walnut. The mass of each walnut may be harder to assess quickly than a constant or gradually changing characteristic such as substrate hardness or intensity of kleptoparastism. Overall, we were successful in predicting many qualitative aspects of walnut-dropping behavior by American crows. This suggests that these crows have evolved or learned to maximize the energy obtained from each dropped walnut. Thus, American crows feeding on walnuts, and avian prey-dropping in general, provides an excellent system for future studies of the ontogeny of a complex behavior and the process of prey assessment.

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