SHELL DROPPING: DECISION-MAKING AND OPTIMAL FORAGING IN NORTHWESTERN CROWS

by

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(With 4 Figures)
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INTRODUCTION

The past few years have seen an explosion of theoretical work on optimal foraging. Reviews appear in PYKE, PULLIAM & CHARNOV (1977) and NORBERG (1977). Of particular interest have been prey selection, exploitation of patchy food supplies, and energetics of foraging and feeding. Optimal foraging frequently implies that animals are capable of sophisticated behaviour involving subtle discriminations and decision-making. Little information is available on these topics except from laboratory experiments and other relatively simple systems involving hummingbirds and other nectarivores.

Dropping of shelled molluscs by gulls and crows is ideally suited for investigating discrimination and decision-making in terms of optimal foraging. In a recent paper I described the behaviour of Northwestern crows (*Corvus caurinus*) dropping whelks (*Thais lamellosa*) on Mandarte Island, B. C., Canada, (ZACH, 1978). Briefly, crows fly to the beach and search for whelks in the intertidal zone near the water. Once a suitable whelk is found, they carry it towards the land and drop it from a height for breaking. This characteristically involves a horizontal flight followed by an almost vertical ascent and then the drop. The vertical ascent and drop are repeated until the whelk breaks. Crows rarely give up even if a whelk has to be dropped many times. Crows take only the largest whelks and they switch to other food rather than to smaller whelks when no large ones

can be found. Crows have specific dropping sites where whelks can be dropped onto rock and where whelks are unlikely to bounce into the water and out of reach. Before and after breaking whelks, crows usually perch in bushes and trees beyond the beach.

This study addresses the following questions. (1) Why do crows select only large whelks for dropping? (2) Why do crows not give up and search for a new whelk if a particular one does not break readily? (3) Do crows drop whelks from the best height for breaking? (4) How energetically profitable is dropping of whelks?

METHODS

I observed five pairs of territorial crows foraging on separate sections of a beach. I timed the following activities ($\pm$ .1 s): flight from perch to water (1), search for whelk (2), flight to dropping site and first drop (3), handling of whelk between drops (4), subsequent drop (5), extraction of animal following last drop (6), flight back to water (7), or flight back to perch (8). These activities are summarized in Fig. 1. I also counted the number of whelks broken per visit to the beach. Data for number of drops required for breaking whelks and height of drop were taken from ZACH (1978).
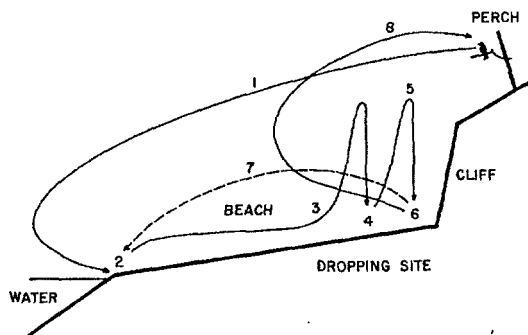

Fig. 1. Schematic representation of activities of crows while dropping whelks. Flight from perch to water (1), search for whelk (2), flight to dropping site and first drop (3), handling of whelk between drops (4), subsequent drop (5), extraction of animal following last drop (6), flight back to water (7) and flight back to perch (8). Most whelks required several drops before breaking. Crows took from 1 to 3 whelks per visit to the beach. If only one whelk was taken, flight back to the water (7) did not occur.

IRVING, KROG & MONSON (1955) determined the basal metabolic rate (BMR) of Northwestern crows. I used their summer value of .85 cal/s together with multipliers (KING, 1974) to convert time budgets into energy budgets. I used 1.5 BMR for perching or resting. 2 BMR was used for standing during handling whelk between drops and extraction of animal following last drop. I used 3 BMR for slow walking during search for whelk. Similar values for resting, standing, or walking birds have been used by SCHARTZ & ZIMMERMAN (1971), CUSTER & PITELKA (1972), UTTER & LeFEBVRE (1973), and FEDAK, PINSHOW & SCHMIDT-NIELSEN (1974). BERNSTEIN, THOMAS & SCHMIDT-NIELSEN (1974) determined energy requirements for level flight in fish crows (*C. ossifragus*). Since fish crows and Northwestern crows are comparable in size (GOODWIN,

1976) I used 9 BMR for flight as determined from their data. LeFebvre (1964), Tucker (1968, 1969), Utter & LeFebvre (1970), Schartz & Zimmerman (1971), and Custer & Pitelka (1972) have found or used similar values for flying birds. However, crows did not always fly horizontally (Fig. 1). Level flight is more costly than descending flight and less costly than ascending flight (Bernstein, Thomas & Schmidt-Nielsen, 1974). I assumed that all flight was horizontal, reasoning that differences in costs of ascending and descending flight are compensatory. Since crows made no net gains or losses of height during visits to beach (see Fig. 1), these assumptions are not unreasonable.

Data for size of whelks dropped by crows were taken from Zach (1978). I collected a sample of 58 live whelks of about the same size as those broken by crows to determine dry weight. Shell length was unsuitable to predict dry weight because many of the shells left by crows had broken off spires. Therefore, I took a measurement (b) across the base and opening of shells (Zach, 1978). I then extracted animals from shells and removed opercula. Animals were dried to constant weight for 48 h at 60°C and weighed ($\pm$ .1 mg). I computed a regression equation to predict dry weight (dw) of animals of whelks dropped by crows (dw = .0812 b3 — .0673, r = .75, Bartlett's three group method for model II regression, Sokal & Rohlf, 1969). I also collected a sample of smaller whelks to determine dry weight of animals of whelks ignored by crows. These whelks were handled in the same manner but no regression equation was calculated. For caloric conversions I used 4.98 kcal/g dry weight, a value determined by Menge (1972) for *T. lamellosa.*

I erected a 15 m high pole on the beach from which I could drop whelks to determine height required for breaking. The pole had a pulley with a small platform from which whelks could be released from various heights. Whelks fell on rocky substrate comparable to that of sites used by crows. I dropped whelks of three discrete size classes differing in shell length: small (1.6-2.2 cm), medium (2.7-3.3 cm) and large (3.8-4.4 cm). Large whelks were similar to whelks selected by crows for dropping. Medium and small whelks were ignored by crows (Zach, 1978). I dropped 12 whelks of each size class from 2, 3, 4, 5, 6, 7, 8, 10 and 15 m. Each whelk was dropped 10 times or until its spire broke off.

RESULTS

Before examining the questions posed above I had to determine exactly when crows stopped dropping a given whelk. Shells broken and left by crows can be grouped into two classes: spire off, and one or more whorls open (see Zach, 1978). From shells with broken off spires, crows can extract animals readily. This is not always the case from shells with opened whorls. Frequently the spire breaks off directly. However, sometimes one or more whorl opens first. The question is, how many of these whelks are dropped again until the spire breaks off.

Of a sample of 90 freshly broken shells collected from dropping sites, 68 (75.6%) had broken off spires and 22 (24.4%) one or more whorls open. I compared these values with those obtained from dropping large whelks from the pole over the range of heights (3, 4, 5, 6 and 7 m) used by crows. Out of 60 whelks, 56 broke. Of these 29 (51.8%) had broken off spires and in 27 (48.2%) one or more whorls opened first. Thus, crows left a greater proportion of whelks with broken off spires than expected from the pole data ($P < .005$, single classification goodness of fit test). This indicates that they

dropped approximately 50% of the whelks, in which first one or more whorls opened, again until the spire broke off. I took this into consideration when computing number of drops required for breaking whelks dropped from the pole. Crows obtained most or all of the animal of dropped whelks (ZACH, 1978).

Dropping from pole.

Large whelks broke much more readily than medium and small ones (Fig. 2). They required fewer drops for breaking at all heights. There was no threshold height above which all whelks of a given size broke on the first drop. Probability of breaking depends on size of whelk and height of drop. In practice, substrate does not affect this probability greatly because crows drop whelks selectively on rock (ZACH, 1978).
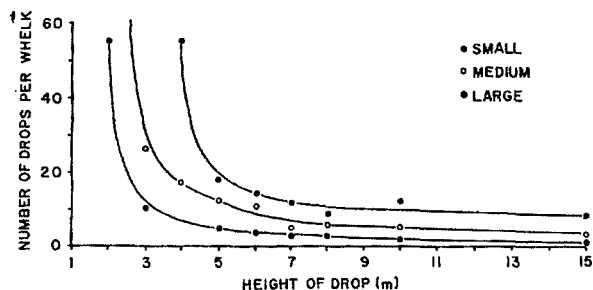

Fig. 2. Mean number of drops required for breaking large, medium and small whelks dropped from various heights from pole. Curves fitted by eye.

As in other locations whelks on Mandarte Island are very variable in shell form and amount of ornamentation (see GRIFFITH, 1967). They also differ in degree of wear. This implies that some may be much more difficult to break than others. Thus, if a sample of whelks is dropped, percentage breaking over successive drops should decrease because an increasing proportion of the unbroken whelks are hard to break. Alternatively, if shells gradually weaken before breaking, percentage of whelks breaking should increase. For large whelks dropped over the range of heights used by crows, percentage of whelks breaking over successive drops remained relatively stable (Fig. 3). The seemingly drastic decline over the last two drops did not indicate a significant trend since only four whelks were left unbroken. These results show that probability of breaking remains about the same over successive drops. Apparently, all large whelks are approximately equally likely to break. Further, shells do not seem to weaken if dropped repeatedly.

I dropped samples of 25 large whelks from about 5 m on rock, water and

grass, substrates readily available to crows for dropping. Seven of the whelks dropped on rock broke. None of those dropped on water or grass broke. Thus, rock, the substrate selected by crows (ZACH, 1978), is best for breaking whelks.
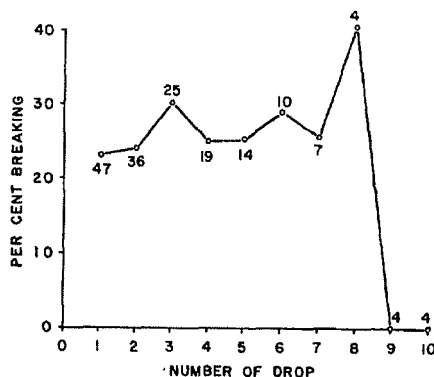

Fig. 3. Percentage of large whelks breaking over successive drops from pole. Data were combined of whelks dropped from 3, 4, 5, 6, and 7 m. Numbers are whelks left unbroken out of a total of 60. Percentages are based on these values.

Dropping by crows.

Steep ascending flight during dropping of whelks is energetically expensive (see BERNSTEIN, THOMAS & SCHMIDT-NIELSEN, 1974). Therefore, if crows are to break whelks efficiently, ascending flight should be minimized. Thus, they must choose height of drop carefully.

Total amount of ascending flight required to break a whelk from a given height can be quantified by the product of hight of drop and the mean number of drops required for breaking. Curves obtained are basically U-shaped (Fig. 4). Crows dropped whelks from an average height of 5.23 $\pm$
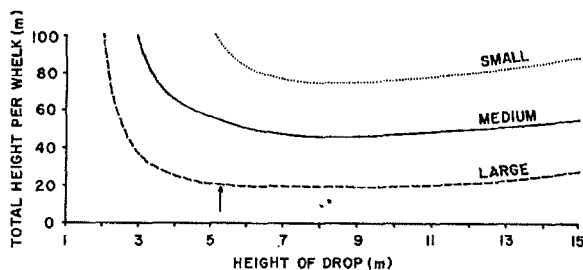

Fig. 4. Total height required for breaking small, medium and large whelks dropped from various heights from pole. Arrow indicates mean height used by crows. Curves fitted by eye.

.07 m (N = 189). This value is where the curve for large whelks approaches its minimum value (Fig. 4). Thus, it is exactly where one would expect it to be if crows attempted to minimize ascending flight.

Time and energy budget.

Durations of activities during dropping of whelks are summarized in Table 1. Crows broke $1.52 \pm .11$ (N = 42) whelks per visit to beach. On the average, whelks required $4.36 \pm .39$ (N = 72) drops to break. Taking these values into consideration, crows expended .55 kcal per whelk. Mean dry weight of animals of whelks broken by crows was $.41 \pm .01$ g (N = 76). This translates to 2.04 kcal. Thus, the net energy gain was 1.49 kcal per whelk broken. If only one whelk is taken per visit to beach, as was commonly the case, this value would be reduced to 1.46 kcal.

TABLE 1

Time and energy budget of dropping of whelks by crows

| | | Time budget | | Energy budget | |
Activity	N	Time (s)	Total time (s)	cal/s	cal
1. Flight from perch	37	$7.02 \pm .44$	7.02	7.65	53.70
2. Search for whelk	42	31.05 ± 3.74	47.20	2.55	120.36
3. First drop	37	$6.88 \pm .30$	10.46	7.65	80.02
4. Handling between drops	62	25.08 ± 3.41	128.09	1.70	217.75
5. Subsequent drop	41	$4.69 \pm .22$	23.95	7.65	183.22
6. Extraction	42	43.20 ± 4.70	65.66	1.70	111.62
7. Flight back to water	38	$3.97 \pm .24$	2.06	7.65	15.76
8. Flight to perch	46	$7.69 \pm .37$	7.69	7.65	58.83
Total			292.13		841.26
Total per whelk			192.19		553.46

Energy budget is based on mean number of whelks broken per visit to beach ($1.52 \pm .11$) and mean number of drops required for breaking ($4.36 \pm .39$).

How much energy could crows gain by breaking medium whelks? Assuming search time is the same as for large whelks and that they break one whelk per visit and drop whelks from the height requiring least ascending flight (see Fig. 4), they would have to expend .90 kcal per whelk. Mean dry weight of animals of medium whelks was $.12 \pm .01$ g (N = 15). Thus, each whelk would yield .60 kcal. Therefore, taking medium whelks would result in a net energy loss of .30 kcal per whelk. Even if search time for medium whelks is much shorter than for large ones (Table 1), which is unlikely since whelks of all size classes are approximately equally available (see ZACH, 1978), net gain would remain virtually unaffected. Crows would lose even more energy

by dropping small whelks because these are more difficult to break than medium ones (Fig. 2). Further, each small whelk would yield only about .11 kcal.

DISCUSSION

Most optimal prey selection models assume that predators can rank prey types according to profitability and that only profitable prey are included in the diet. Profitability is usually equated with energy gained per unit searching effort. Predators may maximize energy gained or minimize search time (SCHOENER, 1971). Thus, optimal prey selection and energetics of foraging and feeding behaviour are closely interrelated and must therefore be considered together.

Crows select only the largest whelks available for breaking (ZACH, 1978). Results of this study clearly show that this is energetically advantageous. Large whelks have a higher caloric content than medium and small ones and also break more readily (Fig. 2). Therefore, they are more profitable provided search times are similar. Crows can gain net energy only by dropping large whelks. This explains why they not only prefer large whelks but also fail to switch to smaller ones even if no large ones are available (ZACH, 1978). Kelp gulls (*Larus dominicanus*) also selectively drop large black mussels *(Choromytilus meridionalis)*, which break more readily than smaller ones (SIEGFRIED, 1977).

To make a profit, crows must select and drop whelks carefully, as the cost of breaking decreases with increasing size. Further, dry weight and caloric content are approximately cubic functions of shell length. This means that profitability decreases rapidly with decreasing size of whelks. Crows probably choose whelks first by sight and then by weight (ZACH, 1978). Before accepting a whelk for dropping, several are picked up with the bill and laid down again. Thus, crows apparently "test" whelks before making a final selection. This is similar to prey selection by wolves and hyenas (MECH, 1970; KRUUK, 1972). Investing energy in selecting prey is adaptive if handling and/or pursuit are relatively costly compared to search.

Many studies of foraging behaviour have demonstrated some form of selectivity (CURIO, 1976), but few have examined the energetics of selectivity. KEAR (1962), HESPENHEIDE (1966), WILLSON (1971), WILLSON & HARMESON (1973) and ABBOTT, ABBOTT & GRANT (1975) have investigated seed selection in a variety of birds. In general, birds preferred seeds that could be handled readily and were highly profitable. However, there were many exceptions. Apparently, predators cannot always rank prey types according to profitability even in relatively simple situations. It is also possible that purely

energetic measures of profitability, which exclude such factors as palatability and specific hungers are inadequate (ZACH & FALLS, 1978).

Crows are very persistent in attempting to break whelks. One crow dropped a whelk 20 times before breaking it and spent 1.81 kcal. Thus, net energy gained is only .23 kcal. Since only a fraction of energy gained is assimilated (see below), breaking this whelk resulted in an energy loss. Why do crows not give up if a whelk does not break within a critical number of drops?

The reason for this is shown in Fig. 3. The percentage of large whelks breaking over successive drops stays about the same. Thus, a whelk already dropped several times is just as likely to break on the next trial as one dropped for the first time. This suggests that dropping of whelks is a stochastic process with probability of breaking dependent on size of whelk, height of drop and type of substrate. Crows can increase profitability by selecting the largest whelks available for breaking, by minimizing ascending flight during dropping, and by dropping on rock only. However, one crow found yet another way. It sometimes carried and dropped two whelks simultaneously (ZACH, 1978).

Giving up after exceeding a critical number of drops would be energetically advantageous only if the probability of breaking decreases over successive drops. If this were the case, the decisions confronting crows would be analogous to those confronting predators foraging in food patches of diminishing profitability, that is, when to give up and move on to the next patch (KREBS, RYAN & CHARNOV, 1974; ZACH & FALLS, 1976). Since whelks are very patchy in distribution, crows are likely confronted with this type of decision while searching for them on the beach. Thus, optimal foraging implies use of a "giving-up" criterion while searching for whelks but not while dropping them.

Crows apparently minimized total amount of ascending flight when choosing height of drop (Fig. 4). However, the total amount of ascending flight remains low over a considerable range of height of drop (Fig. 4). Further, handling whelks between drops involves a substantial amount of time and energy (Table 1). Therefore, crows could have reduced number of drops and increased profitability by increasing height of drop without increasing total amount of ascending flight.

There are several reasons why increasing the height of drop is not advantageous. Crows seem to have difficulty finding dropped whelks because sites used for dropping are usually littered with shell fragments (ZACH, 1978). Increasing height of drop would decrease efficiency of finding because dropping and bouncing whelks become more difficult to see. Bouncing would also increase. Further, whelks dropped from greater height tend to shatter

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and soft parts spill out. Several crows were seen dipping broken whelks in fresh water puddles before eating. This may have helped to remove undesirable shell chips.

For each whelk broken, crows expended .55 kcal, and gained 2.04 kcal. Thus, assuming an assimilation efficiency of 70% (HAINSWORTH, 1974; RICKLEFS, 1974; WIENS & NUSSBAUM, 1975) energy gained would suffice to break 1.5 additional whelks. Similarly, each whelk would yield sufficient energy for 12 min of perching or to fly a distance of 1.1 km (see BERNSTEIN, THOMAS & SCHMIDT-NIELSEN, 1974). Achieved foraging efficiency (WOLF, HAINSWORTH & GILL, 1975) of dropping of whelks is 2.04 kcal/.55 kcal = 3.71. Assuming that prey types do not differ greatly in assimilation efficiency, this is probably the most useful way of expressing profitability and behavioural efficiency. It allows us to make both intra and interspecific comparisons.

Crows broke one, two, or three whelks per visit to beach. The corresponding efficiencies are 3.52, 3.78 and 3.87, respectively. Thus, efficiency is not greatly affected by length of foraging bout. This is because flights to and from the beach and from dropping sites to the water are relatively short (Fig. 1, Table 1). If these flights were longer, optimally foraging crows should always have broken the maximum number of whelks possible per visit to the beach. The maximum number of whelks is probably determined by the size and degree of emptiness of the crop and proventriculus.

How does an achieved foraging efficiency of 3.71 compare with values attained by other birds? Two male malachite sunbirds (*Nectarinia famosa*) observed by WOLF (1975) had achieved foraging efficiencies of 4.25 and 3.43, respectively. Under comparable conditions hummingbirds would have lower values (WOLF, HAINSWORTH & GILL, 1975) due to higher foraging costs. Achieved foraging efficiency of male Rivoli's hummingbirds (*Eugenes fulgens*) ranged from 1.84 to 2.33 repending on the number of flowers visited per foraging bout (WOLF, STILES & HAINSWORTH, 1976). Actually, the foraging efficiencies reported for these nectarivores are somewhat higher relative to the value for crows because assimilation efficiency of nectar is higher (see HAINSWORTH, 1974) than for whelks. Thus, foraging efficiency of crows dropping whelks falls between values for hummingbirds and sunbirds. High achieved foraging efficiencies are important because they can result in a reduction in the percentage of day spent foraging. Thus, birds may have time and energy for relatively expensive activities such as territoriality.

Unlike hummingbirds and sunbirds, Northwestern crows are catholic in their diets (GOODWIN, 1976). Thus, foraging efficiency may be quite variable.

Frequently, different prey types such as birds' eggs and young, berries and invertebrates are found in different places and demand different foraging techniques (CROZE, 1970; MONTEVECCHI, 1976). Sometimes crows do not drop whelks even if many are available. At other times many whelks are dropped. Presumably, frequency of dropping of whelks reflects profitabilities of other prey types. Unfortunately, these profitabilities are difficult to determine because crows are often unobservable. However, to forage optimally predators must evaluate all prey types constantly and feed on the most profitable one (ROYAMA, 1970; TULLOCK, 1971; OSTER & HEINRICH, 1976).

Crows achieved close to the maximum foraging efficiency possible for breaking whelks. To do so, they had to make several important decisions: choosing only large whelks; dropping them on rock only; choosing the best height for dropping; and dropping whelks until breaking. Making wrong decisions would have drastically affected foraging efficiency. Crows are well known to be relatively intelligent (TINBERGEN, 1953; CROZE, 1970; POWELL, 1972), and dropping behaviour appears to be learned (ZACH, 1978). Learning can be very important in optimal foraging because it allows modification and adjustment of behaviour. However, in completely predictable situations, optimal responses may become genetically encoded and thereby lose flexibility. This could lead to sub-optimal foraging if predators respond to inappropriate stimuli.

SUMMARY

Decision-making and optimal foraging was investigated in Northwestern crows (*Corvus caurinus*) feeding on whelks (*Thais lamellosa*).

Crows foraged on whelks by dropping them from a height for breaking. This foraging pattern is a stochastic process; the probability of breaking depends on height of drop, size of whelk and type of substrate. Large whelks selected by crows broke more readily than medium and small ones. They also had a higher caloric content. Crows minimized total amount of ascending flight required for breaking whelks when choosing height of drop. This was advantageous because ascending flight was energetically expensive. Crows dropped individual whelks repeatedly until they broke. This was profitable because percentage of whelks breaking over successive drops remained relatively stable. Thus, it was not beneficial to go in search of another whelk if a given one did not immediately break. All whelks were dropped on rock, the best substrate available for breaking. Crows made a net gain of 1.49 kcal per whelk dropped, sufficient to break an additional 1.5 whelks. Dropping medium and small whelks would have resulted in a loss of energy because these whelks broke less readily and also had a lower caloric content than large ones. Achieved foraging efficiency was 3.71. This is close to the maximum value attainable for crows. Foraging efficiency was relatively insensitive to length of foraging bout and crows took from one to three whelks per bout.

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ZUSAMMENFASSUNG

Entschlussfähigkeit und optimalisierte Futtersuche einer Krähen Art (*Corvus caurinus*) beim Zerbrechen von Muscheln (*Thais lamellosa*) wurde studiert.

Die Krähen ernährten sich von Muscheln indem sie diese aus Flughöhe fallen liessen, um sie aufzubrechen. Die Futtersuche ist ein stochastischer Vorgang; die Zerbrechwahr-scheinlichkeit hängt ab von der Fallhöhe, der Grösse der Muschel und der Art des Bodens. Die von den Krähen ausgewählten grossen Muscheln zerbrachen leichter als diejenigen mittlerer oder kleinerer Grösse. Diese Muscheln hatten auch einen höheren Kalorien-gehalt. Um das Aufbrechen der Muscheln zu erreichen, wählten die Krähen eine minimale Flughöhe. Das ist von Vorteil, da aufsteigender Flug energetisch ungünstig ist. Die Krähen liessen manche Muscheln wiederholt fallen, solange bis sie zerbrachen. Auch das war von Vorteil, da der prozentuale Anteil von Muscheln, der während einer Reihe von Fallversuchen zerbrach, relativ konstant war. Es war daher nicht vorteilhaft nach einer anderen Muschel zu suchen, wenn eine vorhandene nicht unmittelbar zerbrach. Alle Muscheln wurden auf Felsen fallengelassen, welcher der am besten geeignete Teil der Erdoberfläche für das Aufbrechen ist. Pro fallengelassene Muschel machten die Krähen einen Nettogewinn von 1,49 Kcal, genügend, um weitere 1,5 Muscheln aufzubrechen. Das Aufbrechen von Muscheln mittlerer oder kleiner Grösse hätte zu einem Energieverlust geführt, da diese nicht so leicht zerbrechen und da sie weniger Kalorien enthalten als die grösseren. Der erreichte Nutzeffekt war 3,71. Das ist nahe am Maximalwert, den Krähen erreichen können. Die Effektivität der Futtersuche war relativ unempfindlich in bezug auf die Länge der Suchsequenz, die Krähen nahmen ein bis drei Muscheln pro Sequenz.