TEMPORAL AND ENERGETIC ASPECTS OF FOOD STORAGE IN NORTHWESTERN CROWS

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CONTENTS

1. INTRODUCTION

The Northwestern Crow *Corvus caurinus* is a common scavenger and predator found along a narrow coastal strip from Washington to Alaska (Godfrey 1966). Although catholic in its feeding habits, the vast majority of its food comes from the intertidal zone (Butler 1974). Observations have shown that the species stores large quantities of this intertidal food, such as clams, crabs and fish.

In a previous paper (James & Verbeek 1983) we described the general aspects of intertidal food storage and recovery in the Northwestern Crow on Mitlenatch Island, British Columbia, Canada. Experiments revealed the relative importance of cache concealment, cache dispersal and food deterioration.

In this paper, we examine the temporal and energetic aspects of intertidal food storing behaviour, with particular reference to seasonal, diurnal and tidal variations.

2. STUDY AREA AND GENERAL METHODS

For a description of Mitlenatch Island and the study area, Camp Bay, see James & Verbeek (1983). The intertidal area and surrounding hillsides of Camp Bay were watched for up to 6 h periods. These periods were distributed over the daylight hours, so that a total daily activity record of food storage behaviour was obtained. The local time was noted for each food item stored and recovered. In addition, crows flying from the beach carrying clams to other parts of the island were noted. For a detailed description of the foods seen stored and recovered see James & Verbeek (1983).

Almost 1500 h of observation were made at Camp Bay from 28 April to 5 September 1979 and 29 April to 6 August 1980. To correlate food storage/recovery activity with tidal parameters, hourly tidal height (m) predictions for Mitlenatch Island were obtained from the Marine Environmental Data Service, Ottawa. By interpolating the local times for storage or recovery events, it was possible to obtain the exact tidal heights corresponding to the events recorded. All statistical tests were taken from Sokal & Rohlf (1969) with significance ascribed at the 5% level. All means are given ± 1 standard deviation.

3. TEMPORAL ASPECTS OF FOOD STORAGE AND RECOVERY

3.1. SEASONAL ASPECTS

The mean number of items stored and carried per hour was highest in May and June and declined steadily toward August (Table I). As the

Table 1. Number (N) and number per hour (N/H) of food items stored, recovered, and carried but not seen stored by Northwestern Crows each month

Month	Stored		Recovered		Carried (clams)	
	N	N/H	N	N/H	N	N/H
April	9	0.75	6	0.33	—	—
May	258	1.08	163	0.75	195	2.03
June	222	1.19	113	0.63	325	4.17
July	96	0.64	75	0.54	99	1.50
August	28	0.52	9	0.25	7	0.39

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Table 2. Number of food items, stored, clams carried but not seen to be stored and food items recovered in relation to the time of day (AM—PM)

Food	Stored and carried			Recovered		
	AM	PM	χ^2	AM	PM	χ^2
Clam (carried)	346	280	6.96^2	—	—	—
Clam (stored)	247	195	6.11^1	83	229	68.32^3
Unidentified	24	43	5.39^1	4	20	10.67^3
Crab	23	18	0.61n.s.	3	10	3.77n.s.
Fish	6	22	9.14^3	—	11	11.00^3
Human refuse	4	5	—	1	2	—
Nereid	1	7	—	—	—	—
Berry	4	3	—	—	1	—
Ants	—	6	—	—	—	—
Gull regurgitation	1	2	—	—	—	—
Snake	1	1	—	1	—	—
Bone	—	—	—	—	1	—
Total (Stored and recovered)	311	302	0.13n.s.	92	274	90.50^3

^{1}: $p < 0.025$; ^{2}: $p < 0.01$; ^{3}: $p < 0.005$; d.f. = 1

number of items recovered is a function of those stored, a similar pattern is found in the recoveries, although the peak for recoveries occurred in May, as opposed to June for storage and carried items.

3.2. DISCUSSION

Of the alternative sources of food, eggs of the Glaucous-winged Gull *Larus glaucescens* were present from late-May to late-July while gull chicks and regurgitated food items were available from late-June onward (pers. obs.). Meadow invertebrates were most abundant at the beginning of July (Butler 1979). Prior to the availability of these alternate sources of food, the Northwestern Crow on the island depends mostly on intertidal organisms. They peak in abundance at the beginning of June (Butler 1979), and are only available during low tide, hence the need to cache them to ensure a food supply at high tide. As the season progresses, and alternative food (meadows and seabirds colonies) becomes more abundant, the need for intertidal food storage diminishes. Egg-laying in the crow is completed by the middle of June (Butler 1979, pers. obs.), hence the females's energetic requirements for egg formation and incubation are derived from intertidal foods. Several times males were seen to recover stored food and feed it to their mates. It thus appears that stored food is important to the reproductive success of the crows on Mitlenatch.

3.3. DIURNAL ASPECTS

Significantly more clams were stored or carried elsewhere to be stored in the morning than in the afternoon (Table 2). Fish showed the opposite trend with significantly more cached in the afternoon than in the morning. Overall, food storage occurred equally in the morning and afternoon.

In contrast to the overall pattern seen for food storage, significantly more food recoveries overall occurred in the afternoon than in the morning (Table 2). This holds separately for clams and fish, but not for crabs, which were equally likely to be recovered in the morning or afternoon.

The number of clams carried and food items stored showed a peak in the late morning and around noon, respectively (Fig. 1). Both activities waned through the afternoon with minor peaks occurring between 18.00 and 19.00. In contrast, food recovery occurred mostly in mid-afternoon, with a minor peak showing in the early morning.

3.4. TIDAL ASPECTS

Overall, significantly more food storages occurred on a falling tide (Table 3). Individually, this was true for clams (stored or carried) and crabs, but not for fish. In contrast, significantly more food items were recovered on rising than on falling tides (Table 4).

The overall mean tidal height (3.41 ± 0.73 m)

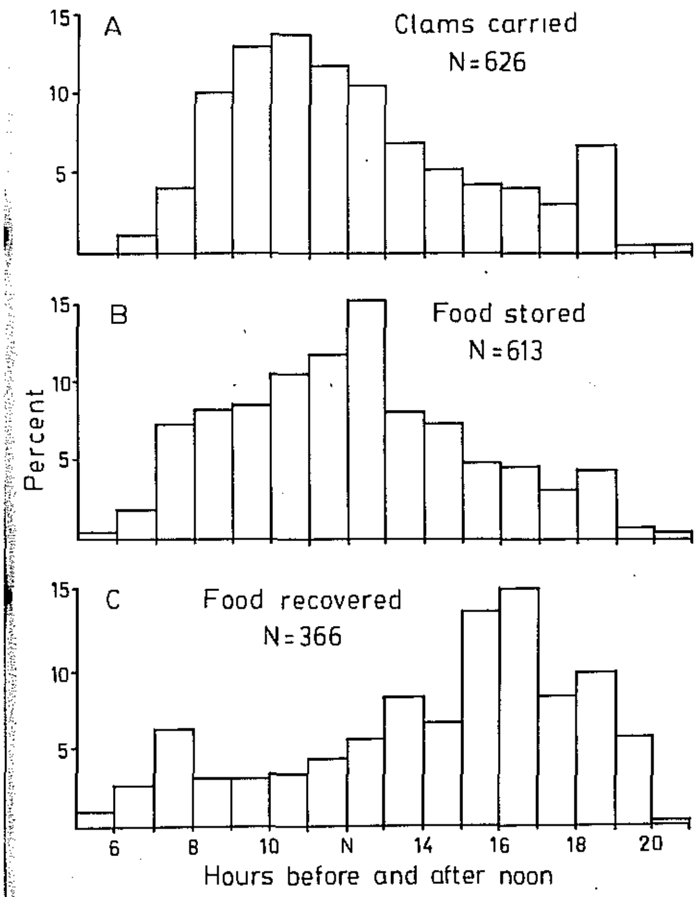

Fig. 1. Diurnal patterns of (A) Clams carried but not seen to be stored. (B) Food stored and (C) Food recovered.

for recoveries (Table 4) was significantly higher ($t = 26.6$, $p < 0.001$) than the corresponding overall mean tidal height for storages 1.98 ± 0.86) (Table 3). The same is true for clams alone ($t = 22.9$, $p < 0.001$).

The pattern of storing food at low tide and recovering it at high tide is shown graphically in Fig. 2. In relation to time before or after low tide, the number of food items stored and clams carried showed a major peak 3—4 h before low tide (Fig. 2). Two major peaks of food recovery occurred, the larger one being in the period following low tide.

The crows followed the falling tide down and first fed on clams at the upper edge of the beach. However, as the tide continued to fall and exposed the algal beds, the crows switched to these and spent their time turning over algae, shells and small rocks searching for hidden prey, such as crabs and fish. An examination of the mean tidal heights at which different food items were stored (Table 3) illustrates this pattern, with clams having the highest value (2.21 m), followed by crabs (1.04 m), nereids (0.94 m) and fish (0.71). In contrast, the recovery of the different food types did not occur at different tidal heights (Table 4).

An examination of Fig. 2 confirms the switch in food types stored discussed above. A peak occurred at 3—4 h prior to low tide for both clams and all item storage. However, the clam peak is significantly larger (proportions test, $t = 3.97$, $p < 0.001$) than the all item peak. In contrast, the peak for all items over the slack low tide period of two hours is significantly larger than the clam storage level then (proportions test, $t = 4.96$, $p < 0.001$).

3.5. DISCUSSION

Regarding individual food types stored, all fish were secured at tidal heights of less than 1 m (Table 3). The number of daylight hours that occurred below this height before noon during

Table 3. Number of food items stored and clams carried in relation to tidal characteristics

Food	Rising tides	Falling tides	χ^2	Slack tides	$\bar{x}$ Height ± S.D. (m) of tide
Clam (carried)	181	418	97.77[3]	27	2.26 ± 0.62
Clam (stored)	94	322	124.96[3]	26	2.21 ± 0.68
Unidentified	17	30	3.60n.s.	20	1.44 ± 0.99
Crab	7	24	9.32[3]	10	1.04 ± 0.55
Fish	6	7	0.08n.s.	15	0.71 ± 0.19
Human refuse	7	2	—	—	2.06 ± 0.62
Nereid	3	2	—	3	0.94 ± 0.21
Berry	4	3	—	—	3.56 ± 0.82
Ants	6	—	—	—	2.26 ± 0.27
Gull regurgitation	3	—	—	—	2.53 ± 0.94
Snake	1	1	—	—	2.15 ± 0.55
Totals (stored)	148	391	109.55[3]	74	1.98 ± 0.86

[1]: $p < 0.025$; [2]: $p < 0.01$; [3]: $p < 0.005$

Table 4. Number of food items recovered in relation to tidal characteristics

Food	Rising tides	Falling tides	χ^2	Slack tides	$\bar{x}$ Height ± S.D. (m) of tide
Clam	180	79	39.39[3]	53	3.40 ± 0.73
Unidentified	17	2	11.84[3]	5	3.68 ± 0.66
Crab	9	2	4.45[1]	2	3.32 ± 0.89
Fish	11	—	5.50[2]	—	3.32 ± 0.48
Human refuse	2	1	—	—	3.00 ± 0.99
Snake	—	—	—	1	4.00 ± 0.00
Bone	—	1	—	—	3.30 ± 0.00
Berry	1	—	—	—	3.50 ± 0.00
Totals	220	85	59.57[3]	61	3.41 ± 0.73

[1]: $p < 0.05$; [2]: $p < 0.025$; [3]: $p < 0.005$

May to July 1979 and 1980 was 27 compared to 96 after noon, a highly significant difference ($\chi^2 = 38.71$, $p < 0.005$). This would account for the temporal fish storage pattern observed in Table 2. The diurnal pattern seen in clam storages can be explained using tidal characteristics. Most clams were stored or carried during a falling tide

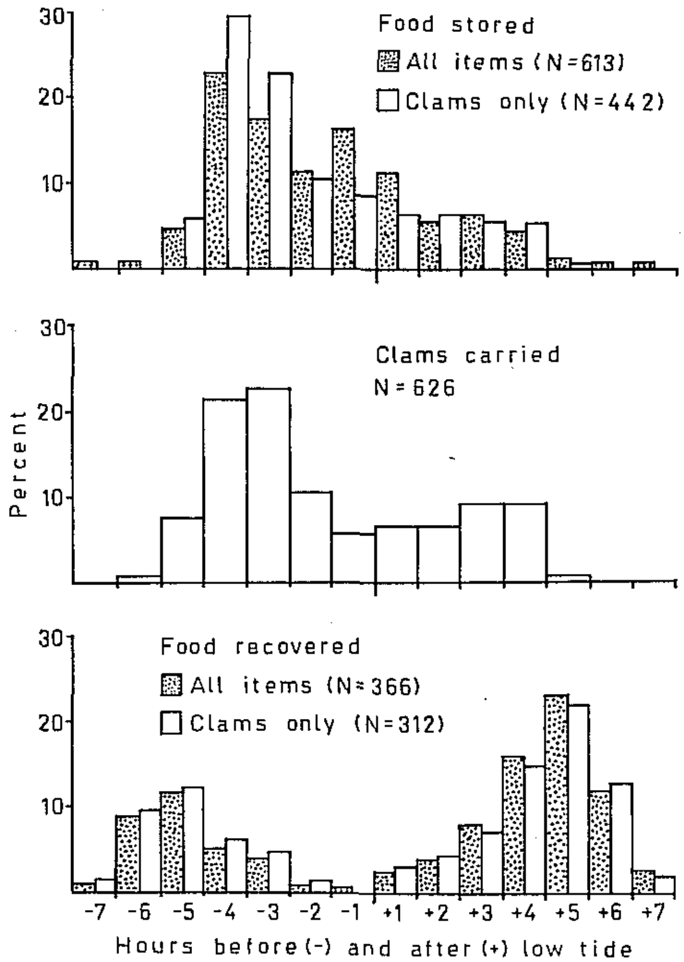

Fig. 2. Frequency of food items stored, clams carried and food recovered in relation to the time before and after low tide.

(Table 3) and falling tides almost always coincided with the morning period.

The reason for the similarity in overall food storages between morning and afternoon (Table 2) is due to the increased storage of items other than clams in the afternoon on rising or slack tides (χ^2 for all non-clam items = 10.81, $p < 0.005$).

As the tide rose in the afternoon, the crows began to recover food (Table 2) before the evening rest period and subsequent roost. The majority of items were recovered before the birds went to the roost, but some remained and were recovered the next morning (Fig. 1).

The hourly analysis of food storages and carried clams (Fig. 1) can be explained by the observations above. More intertidal beach surface is exposed for foraging during the morning period than in the afternoon. During the afternoon, storing and carrying food decline somewhat, because of the rising tide and perhaps the fact that the most easily available items have already been taken. The birds also have, in all likelihood, stored sufficient food for the high tide period later. This is substantiated for several colour-ringed birds, which tended to store the bulk of their caches as the tide fell. In conclusion, then, it appears that the major influence on the diurnal pattern of food storage and recovery is the daily occurrence of ebb and flood.

Little information is available on diurnal patterns of storing food in other species. Verbeek (1972) reported that the Yellow-billed Magpie *Pica nuttalli* only stored acorns in the morning, and Tomback (1977) noted that Clark's Nutcrackers *Nucifraga columbiana* stored seeds all day. Further work is needed to elucidate the daily patterns of food hoarding in other species. Several factors may influence the crow's habit of primarily storing food on a falling tide. Food storage in birds appears to be stimulated by a temporary superabundance of food (Goodwin 1976, Roberts 1979, Turcěk & Kelso 1968). As the tide recedes, it allows access to a large store of potential food. As well as being able to dig animals out of the substrate, the crows can exploit some that are stranded by the tide, such as crabs and fish. The latter prey will not be very plentiful anymore when the tide floods, because most or all of them will already have been eaten by crows and gulls. Thus, it may be the best strategy to hoard the food immediately and eat it later. Additionally, it has been shown (Goodwin 1955, 1976, Gwinner 1965) that when a crow is very hungry, such as after a high tide or night's roost, this promotes food storage.

4. STORED FOOD AND NEST ATTENTIVENESS

As with most corvids (Goodwin 1976), only female Northwestern Crows incubate. During this time a female relies almost entirely on the male to feed her near or at the nest. Once fed, she may leave the immediate area of the nest for a few minutes, usually to defecate, while the male stays at the nest. Following her return, the male leaves to forage again. At high tide early in the season (May and June), when non-intertidal food is relatively scarce, stored food may help to keep the female's attentiveness high (James & Verbeek 1983). The following experiment was performed to test this idea.

4.1. METHODS

Two grounds nests that were about equally far from the beach were selected. The control nest (A) had 4 eggs and the experimental one (B) had 2 eggs. The amount of time the females spent on their nest during a 3h period (nest attentiveness) on each of 3 days was monitored. At the same time a record was kept of how often each male fed his female. On the fourth day, the 2 nests were watched simultaneously in this way by 2 observers from 15.00—18.00 during the high tide period. The following morning, nest B's male was watched as the tide dropped, and each of the 8 clams he stored were immediately removed by us.

The male was visibly agitated at first, although care was then taken not to let him see that each clam was removed. The incubating female was not disturbed and remained on the nest throughout. The male was kept under observation until the beach was covered by the flooding tide. Again, from 15.00—18.00, both nests were watched and nest attentiveness and courtship feeding rates recorded. Finally, as a check, nest B was observed the following day from 16.00—18.00.

4.2. RESULTS AND DISCUSSION

Mean nest attentiveness was 84.7% (N = 10 × 3h records), and it remained high for both nests until the day the stored food was removed (Fig. 3). On that day, during the high tide period, female B's nest attentiveness fell to 53.3% from 76.7% the previous day. Values for the control nest were 88.9% attentive on the day before and 87.2% on the day the food was removed. Furthermore, nest B's attentiveness returned to normal the following day (83.3%). This change in nest attentiveness following food removal is significant ($\chi^2 = 3.89$, $p < 0.05$).

Regarding the number of times the females were fed, females B's feeding rate increased

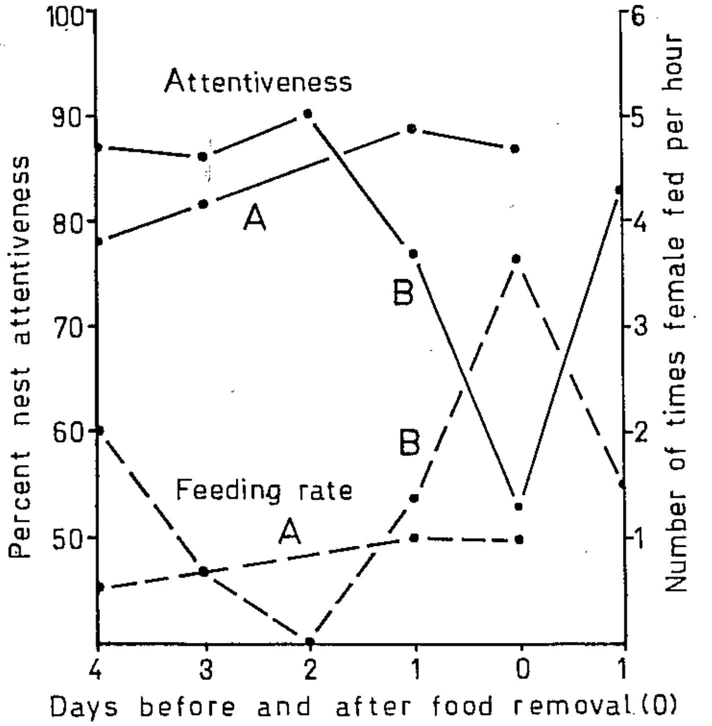

Fig. 3. Nest attentiveness of females A and B and feeding rates by males of females A and B before and after removal of male B's stored food.

quite dramatically from 1.33/h the day before to 3.67/h on the day of the removal of the stored food (Fig. 3), but the change is not significant (Fisher exact test, $p = 0.60$), when compared to the control nest's of 1.00/h on both days. During the high tide period following food removal, the female from nest B once left the nest for an unprecedented 55 min, the most by far any female had. She begged for food constantly, hence the elevated feeding rate (Fig. 3). Nevertheless, she was probably fed insufficiently, as she did not return to the nest. The male actually did recover a clam and fed it partly to her. Presumably it was stored the previous day. For the rest of the time, he visited his caches, but upon finding them empty, he foraged for and fed the female what appeared to be insects. During the same period the previous day, she was fed stored clams on 3 out of 4 times recorded. It appears that stored food is important to maintain high nest attentiveness in the Northwestern Crow during the high tide period. High nest attentiveness probably reduces predation by other crows and also snakes (Campbell 1969).

5. ENERGETIC ASPECTS OF CLAM STORAGE

Despite the wealth of literature on avian food storage behaviour, few attempts have been made to quantify its influence on the life history strategies of the species that exhibit it. Energetic estimates are obviously crude, but allow an indication of the relative importance of stored food to the species involved (Källander 1978, Vander Wall & Balda 1977).

5.1. CLAM SIZE STORED

The most reliable method to determine the sizes of clams stored by crows would be to observe where the caches are made, find them and measure the clams. However, this was impractical on a large scale, as caches were extremely difficult to locate, and hoarding birds might be disturbed. Instead, an indirect method was used.

5.2. METHODS

When walking on the hillsides, we noticed that a large number of intact clam shells were lying about. Both valves were usually connected at the hinge and undamaged. The presence of these shells on the hillsides can be attributed to one or more of the following causes:

1) They were stored by crows and subsequently forgotten.
2) They were stored by crows, but were gaping when recovered, and hence did not need to be dropped to open them.
3) They were stored by crows, but irretrievably lost in a crack or fissure.
4) They were brought to the hillsides by gulls or humans, as no other animals were seen manipulating clams on Mitlenatch. This latter cause can be disregarded almost completely. Gulls did drop bivalves but only on the beach. They were never seen carrying intact clams to the hillsides. People dug clams, but always took them away with them.

During 1980 several days were devoted to searching the hillsides around Camp Bay and elsewhere to collect these double shells.

5.3. RESULTS

A total of 1359 double shells were collected. 1000 *Venerupus* and 359 *Protothaca*. The mean size of *Protothaca* was 3.92 ± 0.70 cm, which is significantly larger (unequal variances t-test, $t = 8.89$, $p < 0.05$) than that of *Venerupus* (3.57 ± 0.43 cm). Butler (1979) reported a mean size of 3.98 ± 0.63 cm, for 250 unspecified clams dropped on crow territories. He noted that these were significantly larger than clams dropped by crows on the beach, suggesting that the crows store the larger shells they find. A few *Saxadomus*, *Macoma* and *Clinocardium* double shells were found, but these were excluded from the analysis.

Do these double shells comprise a representative sample of the total size range stored by the crows? The only cause that may bias this (unless crows forget or lose certain size classes more than others) is if some size classes gaped sooner than others. To test this, 140 clams of different sizes were cached by us. The mean size of clams gaping during the first 48h (3.87 ± 0.37 cm, range = 3.10—4.50, N = 37) was compared to the mean of those that did not gape (3.90 ± 0.48 cm, range = 3.10—5.10, N = 103). Thus, there was no significant difference ($t = 0.35$, d.f. = 138), suggesting that clams were equally prone to gape regardless of size, and that the sample of double shells we collected was representative of what the crows stored.

5.4. CLAM STORAGE AND DAILY ENERGY BUDGET

This section deals with the potential contribution that clam storage makes to the daily energy budget of the Northwestern Crow.

5.5. METHODS

To calculate the daily energy requirements of the crow, we chose the method used by Vander Wall & Balda (1977), who applied it to determine the energetics of seed storage in Clark's Nutcrackers. Firstly, daily existance energy requirements were calculated using the equations of Weiner and Glowacinski (1975). Weights of male and female Northwestern Crows were obtained from Johnson (1961). The mean caloric content of both species of clams were determined by bomb calorimetry.

5.6. RESULTS

On average, a male Northwestern Crow weights 414 g (N = 29) and a female 358 g (N = 11). Mean daily temperature for May and June, when most food was stored was 14 °C. For a male during this period, the daily existence energy is 75.53 kcal, and for a female 69.41 kcal. The cost of free existence was estimated at 40% above existence energy (Wiens and Innis, 1974). Thus, a male required an estimated 105.74 kcal/d, and a female 97.18 kcal/d.

The mean caloric content of clams was 4.68 ± 0.11 kcal/g dry wt for *Protothaca* (N = 18), and 4.72 ± 0.14 kcal/g dry wt for *Venerupus* (N = 9). Because of their close similarity, we decided to pool these values to get an overall mean of 4.69 ± 0.12 kcal/g dry wt of clam. Thus, a stored *Protothaca* of mean size 3.92 cm (= 0.57 g dry wt using Dry Wt = 0.315 Size −0.665, r = 0.888) has a mean caloric content of 2.67 kcal, and a stored *Venerupus* of mean size 3.57 cm (= 0.53 g dry wt using Dry Wt = 0.447 Size −1.07, r = 0.899) has a mean caloric content of 2.49 kcal.

5.7. DISCUSSION

To satisfy his daily needs, a male crow would need to have either 39.6 *Protothaca* or 42.5 *Venerupus*, or about 41 average size clams (= 2.73/h for a 15 h day). As seen before though, the storage strategy is one that circumvents food shortages at high tide. The average period in May and June during which the intertidal food is covered by water (> 3.15 m) is about 6 h. Thus a male needs to store only 6 × 2.73 = 16.4 average size clams.

Observations on three colour-ringed males watched during 10, entire low tide periods showed that they stored an average of 9.1 items, 71.4% (6.5) of which were clams. Thus stored clams contributed about 39.6% of the energy requirement during high tide. Some food items, such as crabs and fish are probably of higher profitability, and these likely make up the deficit. It also seems likely that males should store more than their daily energy requirements in order to feed the female. Catching more profitable items would accommodate this more efficiently too. While we have seen females storing food prior to egg-laying, it is our impression that they do not store as much as the males. Further studies of intersexual differences in food storing are necessary to clarify this point.

Vander Wall & Balda (1977) noted that the Clark's Nutcracker stored from 2.2—3.3 times the necessary energy to survive the autumn and winter months, and attributed the discrepancy to loss by rodents. Tomback (1980) has recently confirmed that they are a major cause of cache loss. The Northwestern Crow's caches were not subject to rodent predation and only a small proportion of the caches were stolen by other crows (James & Verbeek 1983). Over-storing, if it occurs, is thus likely to be in part a response to the needs of the female.

5.8. PROFITABILITY OF CLAM STORAGE

The analysis used was similar to that described by Zach (1979), who measured time budgets in the field and converted them into energy budgets using multipliers (King 1974), in order to investigate the profitability of shell-dropping behaviour in the Northwestern Crow.

5.9. METHODS

We restricted our analysis to clams taken by crows from Camp Bay and stored on the hillside nearby. This standardized flight time as much as possible because no cache site was more than 10s from the beach. We assumed that the clams broke open on the first drop after recovery, which was usually the case.

Irving *et al.* (1955) determined the basal metabolic rate (BMR) of the Northwestern Crow in summer to be 0.85 cal/s. Multipliers were used to convert time budgets into energy budgets (King 1974). 3 BMR was used for slow walking while searching for food, 5 BMR for digging, 9 BMR for flight and 2 BMR was used for the extraction of the flesh after the clam had been dropped (Zach 1979).

5.10. RESULTS AND DISCUSSION

Table 5 shows an approximate time and energy budget for clam storage. While exact times were not measured for all activities, the estimates are considered sufficiently accurate to show the cost of storing relative to the gain.

The total cost per clam (556.2 cal is very close to Zach's (1979) estimated cost of 553.5 cal for dropping whelks *Thais lamellosa*. As shown before, the mean caloric value of the average-sized clams stored was 2.67 kcal for *Protothaca* and 2.49 kcal for *Venerupus*. Thus, the mean net energy gain is 2.11 and 1.93 kcal per clam stored, respectively. The smallest mean-sized clam that should be stored, predicted from the above estimated storing cost of 0.56 kcal is about 2.57 cm. Theoretically, we should not have found any double shells below this size. In fact, only 36 out of 1359 (2.6%) were, so the size of clams cached by the crows is in agreement with the prediction following from our calculation.

Of course, not all of the obtained energy is assimilated. Ricklefs (1974) indicates an assimilation efficiency of 80% for meat and fish diets. Using this value, the crow gains 1.54 kcal (*Venerupus*) or 1.69 kcal (*Protothaca*) per mean sized animal stored. Zach (1979) similarly calculated a net energy gain of 1.19 kcal per whelk broken after assimilation, a substantially lower return. The difference is attributed mostly to the fact that the crows stored larger clam mean dry weights (0.55 g per clam) than they dropped whelks (0.41 g per whelk). In addition, whelks are harder to break than clams, and require several "drops". A calculated mean foraging efficiency (2.58 kcal/0.56 kcal) therefore gives a higher value (4.61) for storing a clam than for dropping a whelk (3.71).

As Zach (1979) noted, Northwestern Crows are diverse in their diets, and foraging efficiencies may be quite variable. This appears to be the case. That food storage is all but abandoned by the Mitlenatch crow population during July and August is presumably indicative of even higher foraging efficiencies in the seabird colonies.

Table 5. Time and energy budget of clam storage by the Northwestern Crow

Activity	N	Time (s)	Cal/s	Cal
Search for clam[1]	79	28.8	2.55	73.4
Dig for clam[2]	—	15.0	4.25	63.7
Fly to hill[2]	—	10.0	7.65	76.5
Search and store	225	24.9	2.55	63.5
Fly to beach[2]	—	10.0	7.65	76.5
Fly to cache[2]	—	10.0	7.65	76.5
Drop clam[3]	37	6.9	7.65	52.7
Extract animal[3]	42	43.2	1.70	73.4
Total				556.2

[1]: Butler (1979); [2]: estimated; [3]: Zach (1979).

6. ACKNOWLEDGEMENTS

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7. SUMMARY

Temporal and energetic aspects of the food storage behaviour of the Northwestern Crow *Corvus caurinus* were investigated on Mitlenatch Island, B.C., Canada. Crows stored predominately marine intertidal food, especially clams, crabs, fish and worms, on the hillsides surrounding the intertidal beach. They also carried food to other parts of the island, presumably to be stored. Food was stored at low tide, and recovered at high tide. Most food was stored in May and June. This seems to be a result of a relative scarcity of non-intertidal food at high tide earlier in the season. During this period too, females are forming and laying eggs, and may depend on stored food at high tide. An experiment confirmed that food stored at low tide was important to an incubating female during high tide, as removal of the stored food caused a significant decline in her nest attentiveness.

Overall, food was stored equally in the morning and afternoon, but clams were stored mostly in the morning. Food recoveries occurred mostly in the afternoon. More food was stored on falling than on rising tides, and vice versa for recoveries. The mean tidal height for food recoveries was significantly higher than that for food storages. A combined hourly tide time analysis illustrates these patterns. The

crow's storage strategy appears to be a short-term tidal one.

The energetics of clam storage was studied. Clam sizes were derived through an indirect method involving collection of double shells. Caloric value of clams was determined by bomb calorimetry, and used to predict the amount of food needed by a crow at high tide. This was compared to observed data. Finally, the profitability of clam storage was investigated, and compared to a similar analysis done on the whelk-dropping behaviour of the species.

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9. SAMENVATTING

We bestudeerden de temporele en energetische aspecten van het voedsel verstoppen van *Corvus caurinus* op het eiland Mitlenatch in Georgia Strait, British Columbia, Canada. Dieren die de kraaien in de laagwaterperiode vingen, vooral schelpdieren, krabben, vissen en wormen, werden op de hellingen langs het strand verstopt. Ze droegen ook voedsel naar andere delen van het eiland, vermoedelijk om het daar te verstoppen. Het voedsel werd bij laag tij verstopt en weer tevoorschijn gehaald gedurende de vloed. Het meeste voedsel werd verstopt in mei en juni. Gedurende deze periode zijn er buiten het wad weinig alternatieve voedselbronnen. Bovendien leggen de vrouwtjes in die tijd eieren en we toonden experimenteel aan dat het verstopte voedsel van belang kan zijn voor het vrouwtje om de continuïteit van het broeden op de eieren te bevorderen.

In het algemeen werd er 's morgens evenveel voedsel verstopt als 's middags. Schelpen werden hoofdzakelijk in de morgen verstopt. Het terugvinden van het voedsel gebeurde voornamelijk in de middag. Er werd meer voedsel verstopt als het water zakte dan wanneer het omhoog kwam; voor het terugvinden van het verstopte voedsel gold het omgekeerde. Het voedsel dat bij laag tij werd verstopt werd gewoonlijk gedurende het daarop volgende hoog tij teruggevonden en opgegeten.

We bepaalden naast de gemiddelde lengte van de verstopte schelpdieren ook de calorische waarde, teneinde te voorspellen hoeveel verstopte schelpdieren een kraai nodig heeft gedurende de periode dat het wad onder water staat. Dit werd vergeleken met het aantal dat in werkelijkheid werd verstopt. Uiteindelijk werden de voordelen van het verstoppen van tweekleppige schelpdieren vergeleken met die van een andere foerageermethode; het stuk laten vallen van wulken.