THE FOOD STORAGE BEHAVIOUR OF THE NORTHWESTERN CROW

by

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(With 2 Figures)
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Introduction

Much attention has been focused on avian food storage behaviour, in terms of the various strategies shown by different species (BALDA & BATEMAN, 1971; BOCK, 1970; BOSSEMA, 1979; CHETTLEBURGH, 1952, 1955; COLLOPY, 1977; COWIE *et al.*, 1981; HAFTORN, 1954, 1956a, b, c, 1974; KÄLLANDER, 1978; KILHAM, 1963; MACROBERTS, 1970, 1975; MACROBERTS & MACROBERTS, 1976; SHERRY *et al.*, 1982; SWANBERG, 1951; TOMBACK, 1977; TURČEK & KELSO, 1968; VANDER WALL & BALDA, 1977), the evolution of the behaviour (ANDERSSON & KREBS, 1978; ROBERTS, 1979; TURČEK & KELSO, 1968), and the problem of how individuals recover their caches (BALDA, 1980; BOSSEMA, 1979; KRUSHINSKAYA, 1970; SHERRY *et al.*, 1981; TOMBACK, 1980; TURČEK, 1966).

Most of the literature on food storage revolves around the behaviour as a long-term seasonal phenomenon, and not as a strategy to accommodate short-term daily food fluctuations. Furthermore, aside from incidental observations, no member of the genus *Corvus* has had its food storage behaviour thoroughly documented (KÄLLANDER, 1978; TURČEK & KELSO, 1968). It is in this light that the following information is presented for the Northwestern crow (*Corvus caurinus*) in coastal British Columbia, Canada.

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Study area and general methods.

The study was conducted on Mitlenatch Island (49°57′N, 125°00′W), Georgia Strait, British Columbia during 1979 and 1980. About 65 pairs of Northwestern crows breed on the island and share it during the summer with among others 1700 pair of glaucous-winged gulls (*Larus glaucescens*), 300 pairs of pelagic cormorants (*Phalacrocorax pelagicus*) and 200 pairs of pigeon guillemots (*Cepphus columba*) (CAMPBELL, 1976).

Most of the study was done in one bay, where the whole intertidal area and surrounding hillsides could be observed from a vantage point. Crows were observed with either 10 × 40 binoculars or 20-45 × telescope for periods of up to 6 h. Data were collected on individually colour-ringed birds and unringed ones. Shifts were alternated, so that over a period of 2 or 3 days, a complete daily activity record of food storage behaviour was obtained. Thus, equal proportions of time were spent observing crows on rising, falling, morning and afternoon tides. The time (P.S.T.) was noted for each food item stored and recovered, and when possible it was identified and the substrate of the cache recorded. Crows flying from the beach carrying clams to another part of the island were also noted. It was assumed that these clams were destined to be stored, as a crow could effectively carry three times more clam viscera for immediate use by breaking clams open first before leaving the beach. As crows were never observed to break a clam and store the viscera, the intact clams carried off were certain to be stored. Only clams carried like this were recorded, not other food items, as we could not be certain these were to be stored.

A stop watch was used to measure how long crows took to hide items. Yearlings that were not colour-ringed could be separated from adults by their browner plumage VERBEEK & BUTLER, 1981). Over 1000 h of observation were made at Camp Bay from 28 April to 5 September 1979 and 29 April to 6 August 1980. All statistical tests were taken from SOKAL & ROHLF (1969) or SNEDECOR (1956) with significance ascribed at the 5% level in all tests unless otherwise stated. All means are given ± 1 standard deviation.

General aspects of food storage and recovery.

Once a food item was procured, the bird flew from the intertidal to the hillside. All foods were transported between the mandibles or in the furcular pouch, never with the feet. Clams were always carried with the umbo pointed forward. Upon landing, a bird walked around selecting a suitable site. Favoured sites included grass clumps, moss banks and the sides of rocks. If a moss bank was selected, the item was put down first and a large beakful of moss pulled out. The food item was then placed in the hole, tapped down with the bill and the moss clump returned to cover the cache. If grass or the side of a rock was chosen, the bird would just push the item down with its beak and pull off nearby vegetation (grass or moss) to cover the cache. Generally, a bird tested one or two places before making a final decision. If another crow was nearby, the caching individual would either wait until the conspecific left, or eat the food immediately. A bird that saw its recently cached item stolen never confronted the thief. KÄLLANDER (1978) reported similar behaviour in rooks (*Corvus frugilegus*). Only 8 out of 376 (2.1%) food items seen stored in 1980 were not covered.

Mobile prey, such as crabs, were either killed by dropping them repeatedly or immobilised by having their legs removed, before storage. In most cases (N = 601) only 1 item was carried and stored, while in a few cases (N = 6) 2 items were carried simultaneously. Five of these cases involved clams and 1, blenny eels, (*Anoplarcus purpurescens*). One colour-ringed 3 year-old male was responsible for four of the two-clam storages. This represented only 5.7% of his total clam storages recorded that season, and 4.8% of his total food storages. The same crow also dropped two clams simultaneously in order to break them open. ZACH (1978) also noted this for certain individuals dropping whelks (*Thais lamellosa*). It thus appears that simultaneous transportation of two food items is a specialised habit, confined to specific individuals. Items that were carried simultaneously were never placed in the same cache. Larger food items, such as some crabs that were transported intact, would be pulled apart on the hillside and cached in several places.

The mean time from when a crow landed to when it left the cache site was 24.90 ± 12.64 sec (N = 225). Eight of these food items were stored by yearlings having a mean storage time of 38.15 ± 21.70 sec compared with 24.42 ± 11.90 sec by 217 adults. The difference is not significant (t = 1.78, unequal variances t-test).

Food was recovered by either walking or flying directly to the cache and exposing it with lateral sweeps of the bill. It was always eaten at the cache site, except clams, which were dropped onto nearby rocks.

Discussion.

The 4 components of hiding acorns in jays (*Garrulus glandarius*) are pushing, hammering, filling-up and covering (BOSSEMA, 1979). Rooks apparently make a hole in the ground before forcefully hammering a nut into it and covering the cache (ANDREW, 1969; KÄLLANDER, 1978; RICHARDS, 1958; SIMMONS, 1970). Clark's nutcrackers (*Nucifraga columbiana*) and Eurasian nutcrackers, (*N. caryocatactes*) also make a hole first before pushing seeds into it, and then covering them (SWANBERG, 1951; TOMBACK, 1977; VANDER WALL & BALDA, 1977). Pinyon jays (*Gymnorhinus cyanocephalus*) use both the bill and feet to expose the substrate, seeds being pushed into the site and covered (BALDA & BATEMAN, 1971). Thus, Northwestern crows quite closely resemble several other corvids in the preparation of the cache site and covering of the food item.

The time taken for a Clark's nutcracker to cache food varies between 10 and 20 sec, depending on the number of seeds cached (VANDER WALL

& BALDA, 1977). The mean of 24.9 sec for the Northwestrn crow may reflect a common adaptation for speed in order to reduce cache loss to other birds. That yearlings store food had also been noted for Clark's nutcrackers (VANDER WALL & BALDA, 1977).

The stimulus for storage to occur need not be satiation of the individual, but the presence of a temporary super-abundance of food (GOODWIN, 1955, 1976; GWINNER, 1965). The possible adaptive value of the behaviour for the Northwestern crow appears to be related to 2 factors. Firstly, storage may offset the relative food shortage at high tide. This is especially true early in the breeding season when alternative foods from the seabirds and terrestrial invertebrates are scarce. Secondly, owing to paucity of food at high tide, stored food may provide a reliable supply of energy to the female when she is forming eggs and incubating. During incubation, when the female relies on the courtship feeding of the male for nourishment, food stored during low tide and recovered during high tide by him may contribute to her high nest attentiveness, with the resultant higher survival of the eggs.

The importance of covering the cache and cache dispersion

The covering of food caches appears to occur universally among corvids (GOODWIN, 1976) and points to its probable importance in camouflaging food. This was tested experimentally in 1979 and 1980. In addition, the dispersion of stored food is important, especially if potential kleptoparasites use area restricted search (TINBERGEN *et al.*, 1967). This was investigated in 1980.

Methods.

Freshly-dug clams were taken from the beach, measured at the widest point to the nearest 0.01 cm, numbered on both valves, and 'cached' on a hillside where several crows stored clams of their own. The method employed was similar to that used by BOSSEMA (1979). About 25 clams were usually laid out at a time along a 16 m nylon line and at different distances up to 1 m from the line. The line was attached at each end to a stake driven into the ground. The microtopography of each cache site was noted and the adjacent portion of the string marked with ink to aid relocation. When all the clams were cached the stakes and line were removed. Care was taken that no crows were watching the procedure. All clams were cached at low tide.

Two sets of experiments employed the above method. In the first, single clams were hidden at each cache site as realistically as crows had been seen hoarding them. A total of 106 clams were hidden during 2 years.

In the second set of experiments, the procedure was repeated, with the difference that clams were left exposed. A total of 131 clams were put out like this during 2 years. All cache sites were checked for the presence of clams every 24 h by replacing the line and stakes and using the combination of ink marks and field notes. All experiments were such that no overlap occurred between them. Six areas were used to lay out clams and were rotated for each experiment.

A third set of experiments involved dispersion. As no crow was ever seen to store more than 1 item in 1 place, 25 clams were cached in 5 groups of 5. All were covered. Caches were about 10 m apart and in each cache the clams were within 10 cm of each other. This was repeated 3 times. No temporal overlap occurred between this and the other experiments. The caches were checked every 24 h.

Apart from crows, no other animals could have removed the clams. Gulls were never seen in the storage area. The only terrestrial mammals on Mitlenatch are deer mice (*Peromyscus maniculatus*) and river otters (*Lutra canadensis*). The latter did not frequent the storage area. To check for possible losses to mice, 5 clams were placed around our cabin within reach of probably the densest population of mice on the island. The clams were checked daily for signs of disturbance, but they remained untouched for 1 week.

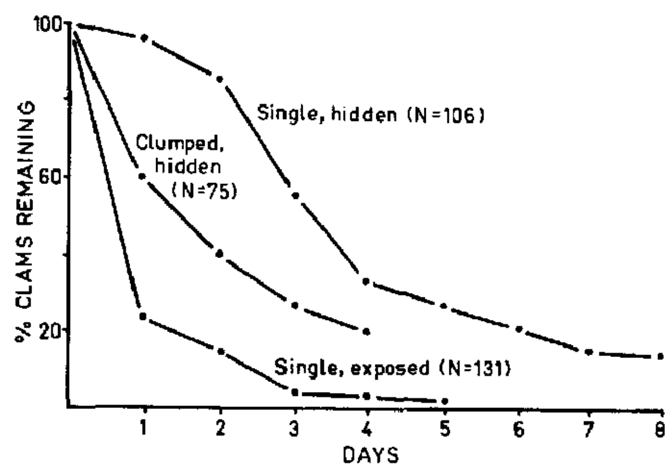

Fig. 1. Percent of clams disappearing as a function of time in three different types of food caches.

Results.

Single hidden clams were found more slowly than exposed ones (Fig. 1). Additionally, single hidden clams disappeared more slowly than clumped, hidden ones (Fig. 1), despite the fact that single clams were more densely distributed than clumped ones (1.28 m^2/cache versus 36.7 m^2/cache, respectively).

The mean survival time per clam in days is significantly different between experimental types ($F = 5.15$, d.f. = 2, $p < 0.05$) but not within replicates ($F = 0.90$, d.f. = 3, n.s.). Single exposed clams disappeared about twice as quickly as single, hidden ones.

Discussion.

Covering the cache significantly enhances the chance that food will not be stolen by other crows. BOSSEMA (1979) showed a similar survival value of covered acorns over uncovered ones for the jay, but whether this was from conspecific competition was not determined. In addition, captive jays took longer to locate single cached acorns than clumped ones (BOSSEMA, 1979) as we found in our study. Jays BOSSEMA, 1979) and marsh tits (*Parus palustris*) (COWIE *et al.*, 1981) never placed more than one item in each cache. SHERRY *et al.* (1982) showed that sunflower seeds stored at high and low densities survive less well than those stored at the intermediate densities in which marsh tits store seeds (COWIE *et al.*, 1981). This suggests the survival of stored items is asymptotic with respect to the density they are stored at.

Storage area used

The Northwestern crow on Mitlenatch Island cached food in exclusive and non-exclusive storage areas. Exclusive storage areas occurred on nesting territories that were defended by mated pairs against other crows. Non-exclusive areas did not form part of territories, were used by several birds, and, while various dominance interactions might take place, the areas were not exclusive to any one individual or pair. The distinction between the 2 types of storage area is not absolute, as some breeding individuals stored food both on their respective territories and on a communal patch.

Because few birds were colour-ringed, it was impossible to assess the size of non-exclusive areas, but they appeared to be much larger than exclusive ones. Similarly, based on a combination of colour rings and morphological features, at least 6 crows, including 2 yearlings and 2, 3 year-old males used a large area. Based on colour-ringed birds, a crow did not use the whole of the non-exclusive storage area, but tended to concentrate stores in parts of it. However, stores did overlap quite broadly with those of other individuals, and these smaller areas of overlap were not defended.

Two colour-ringed males used the same regions within the same non-exclusive area in 1979 and 1980. This suggests that an intimate knowledge of a storage area may help to ensure the successful retention of stored food.

Storage sites used

By observation through a telescope, 230 storage sites were identified (grass 53.0%, moss 21.3%, grass/side of rock 17.0%, moss/side of rock 5.7%, side of rock 1.7%, log 0.9%, rock top 0.4%). Although trees were present, all food storages occurred on the ground, mainly in grass. This pattern generally held true for May, June, and July. Overall, sites without a rock were used significantly more often than those with a rock ($\chi^2 = 60.53$, d.f. = 1, $p < 0.005$). Unfortunately, owing to the scarcity of colour-ringed birds in 1980, it was not possible to collect data on individual storage site preferences of the crows.

Discussion.

Captive jays prefer to hide acorns in soft substrates with a rough surface (BOSSEMA, 1979). Edges (vegetational or textural) were preferred, and there was a tendency to hide food near conspicuous objects. BALDA's (1980) captive Eurasian nutcracker showed a preference for storing seeds close to edges and conspicuous objects, and TOMBACK (1977) noted a strong tendency in Clark's nutcracker in the wild to store food at the base of trees and to avoid hard-packed substrates. A soft substrate allows a food item to be cached quickly and efficiently, and a rough-textured surface may enhance camouflage and serve as a visual guide back to the cache. Grass and moss are soft substrates, but in contrast to grass, moss requires prior excavation before the food is cached and that takes time. Grass may also be a better camouflaging substrate than moss for several reasons. Grass is deeper than moss, and the wind may therefore be less likely to uncover a cache in grass than one in moss. Grass is also less homogeneous than moss, and it is often in motion because of the wind, something that does not occur with moss. A cache placed in moss may therefore be more vulnerable to predation than one placed in grass. To test this idea, we placed 37 clams in moss and 38 in grass. All items were cached singly and covered. After 2 days, 6 grass-placed clams and 18 moss-placed ones had been found by the crows. The grass-placed clams thus remained undetected significantly longer ($\chi^2 = 15.08$, d.f. = 1, $p < 0.005$) than the ones in moss, supporting the hypothesis.

Whether the crows actively selected a grass storage substrate is not known, as the areas covered by each substrate were not quantified.

Foods stored and recovered

Clams, mostly *Venerupus japonica* and *Protothaca staminea* constituted by far the most favoured food storage item (Table 1). Other clams occasionally stored were *Macoma nasuta*, *Saxidomus giganteus* and *Clinocardium nuttalli*.

TABLE 1. Foods stored and recovered[1]) by the Northwestern crow

Food	Stored		Recovered	
	N	%	N	%
Clam (carried)[2])	626		—	
Clam	442	(72.1)	312	(82.5)
Crab	41	(6.7)	13	(3.5)
Fish	28	(4.6)	11	(3.0)
Human refuse	9	(1.5)	3	(0.8)
Nereid	8	(1.3)	—	
Berry	7	(1.1)	1	(0.3)
Ants	6	(1.0)	—	
Gull regurgitation	3	(0.5)	—	
Snake	2	(0.3)	1	(0.3)
Bone	—		1	(0.3)
Unidentified	67	(10.9)	24	(6.6)
Total (Minus clams carried)	613	(100.0)	366	(100.0)

[1]) Items recovered were not necessarily the same ones as those seen stored. [2]) Clams carried inland but whether they were stored could not be seen.

Crabs, *Cancer magister*, *C. productus* and *Pugettia producta* were the next most favoured item with 6.7% of the total stored. All the fishes were blenny eels although BUTLER (1979) recorded sculpins (Cottidae) too. Picknickers visited the island, hence the nine instances of human food stored. Crows also removed and stored meat left on Pacific oysters (*Crassostrea gigas*), which had been opened on the beach by people.

Worms (*Nereis*) were identified on 8 occasions, and berries (*Rubus ursinus* and *Rubus laciniatus*) on 7. Six times in 1979, a colour-ringed 2 year-old male stored dead ants that had been washed up by the tide. Coast garter snakes (*Thamnophis elegans*) were killed with a series of blows to the head. The snakes were then hacked in half by further blows, and each half stored separately. Clearly, the intertidal is by far the most important source of food cached by the Northwestern crow in Camp Bay.

Food items were recovered in roughly the same proportion in which they were stored (Table 1). Clams are somewhat over-represented, and this can be explained by differences in behaviour when recovering different food types. When a crow recovers a clam, it almost always has to drop it onto a hard substrate to break it open. This is a very obvious act compared with the recovery of other food items, where unless one has seen the item stored, one cannot be certain the crow has not just come across some carrion *etc.* This results in non-clam items being underestimated in the analysis.

Discussion.

Camp Bay is unique on the island in having a large, gently-sloping intertidal area with an abundance of marine life. As yet, it is not known if all crows on the island used it. It may be that certain individuals on the island only foraged in the gull colony, cormorant colony or steep rocky intertidal, so that the foods stored will be different in each case.

Although most stored food items were clams, the Northwestern crow also cached a wide diversity of other foods derived from intertidal and non-intertidal sources. Such catholic feeding habits were reported by BUTLER too (1974, 1979) and are typical of the genus (GOODWIN, 1976). In a preliminary analysis of nestling throat samples, BUTLER (1979) found clam viscera to be the most common food item, followed by shore crabs (*Hemigrapsus*) and blenny eels. The shore crab is a very small animal and it probably does not pay energetically to store it.

The crow itself could not choose a better candidate for storage on Mitlenatch than clams. They lend themselves to storage for 3 reasons.

1. They are found most commonly in the upper part of the intertidal zone. While fish and crabs might have a higher net energy yield to the crows than clams, they are found in the lower part of the intertidal zone and hence they are available to the crows for a shorter period than clams are.
2. They are very abundant. BUTLER (1979) found clam (> 5 mm) densities of 181 clams/m^2 within the top 6 cm of the beach substrate.
3. Stored clams do not deteriorate rapidly.

The problem of food deterioration

Rapid deterioration of certain food types has been implied as a factor constraining the evolution of food storage behaviour in certain groups of birds (ROBERTS, 1979). For example, raptorial species exhibit only incipient food hoarding behaviour (COLLOPY, 1977; PHELAN, 1977). When food is stored by raptors it is likely to be for a short time to avoid decay and consumption by invertebrates and bacteria. The Northwestern crow faces similar potential problems when it stores food. To investigate this, an experiment was performed during the 1980 season.

Methods.

Clams (*Venerupus*) were obtained from Camp Bay and each clam (N = 70) was measured across the widest point to the nearest 0.1 mm. The clams were then 'cached' by us in the ground in 14 groups of 5 clams each. Each group of clams consisted of the same approximate size range.

At 7 subsequent periods of 24 h, 2 randomly chosen groups were collected and food competitors (arthropods) found in the clams were noted. The flesh of these clams was air-dried under cheesecloth and then oven-dried at 90°C for 24 h. The dried flesh was weighed to the nearest mg. As the original weights of the clams were not known, a regression equation was calculated for a sample of 30 intact *Venerupus* collected from the beach (Dry weight (g) = 0.447 width - 1.070, r = 0.899). Expected weight values for each of the 70 clams in this experiment were calculated from this, and compared to the actual weights of the experimental clams.

Results.

It took up to 2 days for the majority of clams to gape and permit access to ants (Formicidae), eggs and larvae of flies (Diptera) and wood lice (Oniscoidea). As of the third day, larvae of Diptera were found in 20% of the clams and this rose to 70% by day 6. The weather during the experiment was cool and wet, thus reducing arthropod activity.

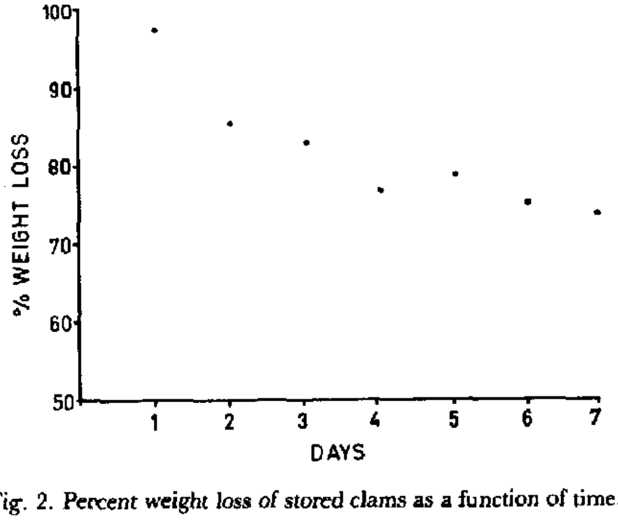

Fig. 2. Percent weight loss of stored clams as a function of time.

The mean weight of clam flesh through the 7 days of the experiment decreased steadily (Fig. 2). The greatest loss to arthropods occurred on the second day when 17.2% of the flesh had been consumed.

Discussion.

The grouping of the clams could have diluted the impact of the arthropod competitors. On several previous occasions, single, hidden clams had been completely eaten by arthropods in 2 days. The 17.2% weight loss that occurred between day 1 and 2 (Fig. 2) could thus have been much higher. It is almost certain that the crows normally do not leave any stored items longer than 2 days (VERBEEK, 1982; pers. obs.). Within the crow's food spectrum, the clam is the best item to store because its valves help to protect it against dehydration and subsequent arthropod depredation. Clams thus may offer the crow the greatest return for its investment. Perhaps not surprisingly, they are the crow's favorite storage item.

Recovery success

Although it was impossible to directly measure the recovery success of stored food through observation because few crows were colour-ringed, an indirect estimate can be attempted. As observations were made throughout the day and summer, the recorded number of storages and recoveries can be considered as a representative sample of the actual totals that occurred, If all food items (Table 1) were considered, this yielded a recovery success of 59.7%. However, as discussed earlier, this figure is biased because clams were recovered in a more conspicuous manner than the other food items. By considering clams only, the recovery success rose to 70.6%.

This estimate can be made more reliable by taking clams stored and recovered by three colour-ringed males under study in 1979. These had a recovery success of 76.0%. This in turn, is a low estimate as it does not allow for clams that do not require dropping as they may have already gaped. These would be less conspicuously recovered than intact clams.

Discussion.

Only 3 other corvids that store food have had their recovery success reported. Of these, the Eurasian nutcracker has been studied the most. Various authors (TURČEK & KELSO, 1968) reported a recovery success of between 6-70%. SWANBERG (1951) estimated 86%, MEZHENNY (1964) and MATTES (1978) noted recovery successes of between 60 and 80%, and BALDA (1980) reported a captive Eurasian nutcracker to have relocated between 39 and 83% of its caches. For the Clark's nutcracker, TOMBACK (1980) estimated a recovery success of between 30 and 72%. Finally, for the jay, BOSSEMA (1979) reported a recovery success of 16%.

These values were calculated either from direct observations of successful and unsuccessful probes, or by comparing the number of probe holes that had open seed hulls near them to those that did not. These methods are partly inaccurate because rodents may feed on the caches, a proportion of the caches is consumed by the birds elsewhere, and birds may not have to probe to recover some caches under objects (BALDA, 1980). However, all of these factors contribute to an underestimate of cache recovery, and so for the nutcrackers at least, recovery success is high. In addition, VANDER WALL & BALDA (1977) calculated that a Clark's nutcracker stores between 2.2 and 3.3 times the energetic requirement for the forthcoming winter, and thus appears to 'anticipate' losses to rodents, *etc*.

The apparently low success rate for the Jay appears to be related to the fact that the birds often carry acorns off to consume them elsewhere (BOSSEMA, 1979). Direct observation is thus required on this species to estimate recovery success, and to establish whether extra food is stored to offset losses to competitors. In this respect, CHETTLEBURGH (1952) noted vast numbers of acorns stored by a group of jays.

The Northwestern crow's food storage habit differs from that of the other seed-storing corvids mentioned because the time between storage and recovery is short. The crow does not appear to store more than is needed for the high tide period, although some stealing does occur. In addition, the number of caches made is small ($N \leq 15$), resulting in reduced probability of caches being forgotten.

The role of olfaction in detecting caches

In general, it is not believed that birds use odour to relocate food caches (BALDA, 1980; BOSSEMA, 1979; SHERRY *et al.*, 1981; TOMBACK, 1980). The following experiment was performed to test whether smell played a role in food recovery by the Northwestern crow.

Methods.

Following the same routine as in the previous experiments, 25 clams were hidden singly on the hillside. Ten of these were filled with either paraffin-wax or putty to the correct fresh weight and glued shut (false clams). The other 15 were freshly dug from the beach. All clams were checked every 24 h, and the experiment replicated 6 times, 3 times each summer, for a total of 60 false and 90 real clams. The false clams had no odour to a human whatsoever, whereas after 2 days out of water, the real clams smelled very strongly.

Results.

Table 2 shows that there was no statistical difference between the number of false and real clams taken by the crows. However, it is only just not significant, so olfaction cannot be ruled out completely.

TABLE 2. Comparison of detection of fresh and false clams by Northwestern crows

	Taken	Not taken
Fresh	52 (46.2)	38 (43.8)
False	25 (30.8)	35 (29.2)

$\chi^2 = 3.74$ n.s. Expected values in brackets.

Discussion.

Olfaction has already been shown to be unimportant for the relocation of stored food in the Eurasian nutcracker (BALDA, 1980), European jay (BOSSEMA, 1979) and marsh tit (SHERRY *et al.*, 1981).

It may be that crows, with their propensity for carrion, have a greater development of the olfactory apparatus than the above species. Even so, we do not believe that Northwestern crows use olfaction to relocate their own food caches, as most are recovered before they smell strongly.

Summary

The food storage behaviour of the Northwestern crow (*Corvus caurinus*) was investigated on Mitlenatch Island, British Columbia. The crows stored mostly 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.

Storage sites included, in decreasing order of importance, grass clumps, moss banks and the sides of rocks. The choice of substrate is discussed in relation to its camouflaging effect. Food items were most often carried and stored singly. Some individuals carried two items at a time. On average, it took a crow 24.9 sec to hide a food item.

The crows stored food in exclusive and non-exclusive areas. Exclusive areas were defended and associated with a nesting territory, whereas non-exclusive areas were not, resulting in several birds using them. Food items were almost always covered and it was shown experimentally that this significantly reduced the chance that the cached item was stolen.

The availability, abundance, profitability and preservation qualities of the stored food were discussed. Storage seems to result from a relative scarcity of non-intertidal food at high tide early in the breeding season. During this period too, females are forming and laying eggs, and may depend on the stored food at high tide.

The success of 3-colour-ringed crows in relocating their food caches was 76%. The birds appeared to have memorized the location of their food stores. Olfaction appeared to be unimportant for the detection of experimentally-hidden clams.

Experiments demonstrated that single stored clams were found more slowly than clumped ones. The problem of stored food decomposition was studied and discussed in relation to the short-term storage strategy.

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Zusammenfassung

Das Verstecken von Nahrung bei der "Northwestern crow" (*Corvus caurinus*) wurde untersucht auf der Insel Mitlenatch, British Columbia, Kanada. Es wurden hauptsächlich Strandtiere versteckt, insbesondere Schaltiere, Krabben, Fische un Würmer. Die Tiere wurden der Küste entlang versteckt. Die Krähen trugen auch Nahrung nach anderen Teilen der Insel, vermutlich auch um sie dort zu verstecken.

Die Nahrung wurde versteckt in Grasklumpen, Moos und an den Seiten von Steinen, in dieser Reihenfolge. Die Wahl der Versteckorte wird in Zusammenhang mit dem Maskierungseffekt besprochen. Die Nahrungsobjekte werden meistens einzelnen getragen und versteckt, und es dauerte durchschnittlich 24.9 Sek um ein Objekt zu verstecken. Fast alle Nahrung wurde bedeckt und es wurde experimentell nachgewiesen dass dadurch die

Möglichkeit dass gestohlen wird vermindert. Angebot, Anzahl, Einträglichkeit und Haltbarkeit der versteckten Tierarten werden besprochen.

Es hat den Anschein dass das Verstecken von Nahrung die Folge einer relativen Knappheit von alternative Nahrung während der Flut am Anfang der Brutsaison ist. In dieser Periode wurde die versteckte Nahrung während der Flut benutzt.

Drei geringte Krähe fanden 76% ihrer versteckten Nahrung zurück. Es zeigte sich dass die Krähe sich erinnern wo sie die Nahrung versteckt hatten. Sie brauchen kein Geruch um experimentell versteckte Nahrung zu finden.