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The mussel caching behaviour of Hooded Crows *Corvus corone cornix*

S. D. BERROW, T. C. KELLY *and* A. A. MYERS *Department of Zoology, Lee Maltings, Prospect Row, University College, Cork, Ireland*

The food caching behaviour of Hooded Crows Corvus corone cornix *was studied at Lough Hyne Marine Reserve, Ireland. All prey items cached were obtained from the intertidal zone and Mussels* Mytilus edulis *were the most frequently recovered prey species. The methods used to cache intertidal prey species were similar to that previously described for other species in the genus* Corvus. *Mussels were cached on a falling tide and usually recovered by crows within 2–3 days. Mussels were recovered during high tide and this behaviour was a response to short-term, daily fluctuations in food availability.*

The hiding or storing of food (caching) is widespread in the Crow family and probably occurs in all species.[1] Although the feeding behaviour of Hooded/Carrion Crows *Corvus corone* has been well studied[2,3] all previous published work on caching in the wild concerned terrestrial prey, or food scraps provided by man.[4–7] Hooded Crows at Lough Hyne consume a wide range of intertidal molluscs and fulfil all the requirements, stated by Roberts,[8] necessary for the evolution of food-storing behaviour. They reside in an environment with periodic pulses of durable, particulate food items (hard-shelled molluscs) followed by periods of relative food scarcity (tidal immersion of foraging areas). They have generalized diets and foraging repertoires, while their territorial behaviour helps individuals retain possession of stored items. James & Verbeek[9] showed that Northwestern Crows *Corvus caurinus* frequently cache prey items obtained from the intertidal zone, during low tide and recover them during high tide. Caches were rarely left for more than 2 days, as loss of flesh to scavenging arthropods increased dramatically after a mollusc had gaped, and this behaviour was shown to be a response to short-term, daily fluctuations in food availability. Intertidal molluscs were the prey items most suitable for caching as they were relatively slow to deteriorate in caches. James & Verbeek[10] showed that bivalve molluscs, that were found intact on hillsides adjacent to the shore, but with valves gaped open, had been previously cached and such foods were important to the reproductive success of Northwestern Crows by increasing nest attentiveness.[10]

The caching of intertidal molluscs by *Corvus corone* has not previously been described. In this paper, we examine the type and size of prey items cached by Hooded Crows *Corvus corone cornix*, and the influence of the tide on this activity. This behaviour is compared with that of Northwestern Crows.[9,10]

MATERIALS AND METHODS

Prey items were collected between January 1988 and December 1989 from the hillside adjacent to the Goleen area of Lough Hyne Marine Reserve, Co. Cork, Ireland (9°18'W, 51°30'N). They were identified, and intact mussel shells were measured. In order to test whether mussel shells recovered from the hillsides were in fact cached, individual mussels of sizes 15–70 mm were artificially cached in grass during February and again in July 1988 and inspected daily. In order to determine the length of time mussels are cached, 20 mussels

(50–60 mm) were marked with paint, after the mussel flesh had been replaced with an equal weight of plasticene to prevent gaping and ensure that they were dropped at dropping sites (roads or rocky shores). These mussels were left on a wall bordering the lough as previous observations had shown that mussels presented in this way were cached when found by crows. Dropping sites were inspected daily for these marked mussels.

A single adult male, colour-ringed Hooded Crow was observed during December 1989 for four consecutive periods of tidal exposure and immersion. The number of prey items cached and dropped in relation to the state of the tide was recorded. A χ^2 test was carried out, using the Yates' correction, on the sum over the 4 days. Some mussels require breaking at dropping sites after being retrieved from a cache. The influence of caching on the dropping height required to break open a mussel was investigated using mussels of 50–60 mm in length. Twenty fresh mussels were dropped by hand from heights of 1–5 m onto a road dropping site until they smashed open and the number of drops required to break open these mussels was compared with mussels that had been artifically cached for 10 days prior to dropping.

RESULTS

Species cached

The distance travelled from collection of a prey item to the cache site was usually less than 100 m. On landing upon the hillside the crow would search for a suitable caching site. Suitable sites were usually clumps of grass at the foot of a rocky outcrop or boulder or occasionally in grass along the road verge. After selecting a suitable site, the crow forced the prey into the grass and then hammered it deeper with its closed bill. The crow would then pull up some adjacent grass and push it into the hole, thus covering the prey item. Often a crow would try 2 or 3 sites before successfully hiding the prey item, but always after only a short walk. Before leaving the site the crow would usually visually scan the area. If a conspecific was in the vicinity the prey item would often be retrieved and the crow would fly off to another site.

Several intertidal species were recovered from hillsides adjacent to the Goleen (Table 1). Most of the bivalve molluscs recovered had gaped with the valves at an angle of 30–45° to each other. Mussels were the most frequently cached prey item, contributing over 90% of the bivalve molluscs cached and 78% of all prey items (Table 1). Hooded Crows at Lough Hyne drop hard-shelled molluscs onto the beach and onto the road adjacent to the lough. The mean size of mussels recovered from the hillside (63.4±0.9 mm, n = 172) was not significantly different from those recovered from the road dropping site (z = 1.11, ns) or the beach dropping site (z = 0.59, ns).

Table 1. Prey items (n = 302) cached by Hooded Crows at Lough Hyne Marine Reserve

Prey species	*Percentage of total (%)*
Common Mussel	78.1
Common Limpet	10.2
Warty Venus	3.6
Edible Periwinkle	2.9
Variegated Scallop	1.6
Carpet Shell	1.0
Shore Crab	1.0
Velvet Swimming Crab	0.7
Common Cockle	0.3
Grey Topshell	0.3

Rate of caching

The mean number of mussels captured by a single male Hooded Crow over over four consecutive diurnal periods of tidal exposure and immersion is shown in Table 2. The number broken open at dropping sites immediately after capture (χ^2_1 = 5.64, $P < 0.05$) and the number cached (χ^2_1 = 13.92, $P < 0.01$) per hour was significantly greater on a receding rather than a rising tide and the rate peaked 1–2 hr before low tide (Table 2). The number of mussels cached per day ranged from 10–12 but there was no significant difference between the numbers cached and those that were immediately broken open at dropping sites (χ^2_1 = 0.79, ns).

Cache recovery

About a half of the cached mussels (45–55%) were retrieved from the cache and smashed at

Table 2. Mean number (±se) of mussels broken open at dropping sites *immediately after capture or cached over a four* consecutive diurnal tidal cycles at Lough Hyne

Period of tidal cycle	*Time (h)*	*Mean number ±se*	
		Dropped	*Cached*
Before low tide	3–4	0	0
	2–3	1.3±0.5	0.8±0.5
	1–2	3.0±0.4	4.8±0.5
	0–1	2.3±0.3	4.5±1.2
After low tide	0–1	1.5±0.6	1.0±0.4
	1–2	0	0
Total		8.0±1.1	11.0±0.6

the road dropping site within 2–3 days of caching though 30% remained cached after 18 days. During February, the artificially cached mussels gaped after 10–15 days while in June they gaped in less than a week. This difference was presumably due to the warmer weather in June. Artificially cached mussels had valves opened at an angle of 30–45°, when they gaped, which was characteristic of bivalve molluscs found on the adjacent hillside.

The number of drops required to artificially break open cached and uncached mussels are shown in Fig. 1. There was a significant relationship between the mean number of drops required to break open a mussel and the height from which it was dropped (Fig. 1), but there

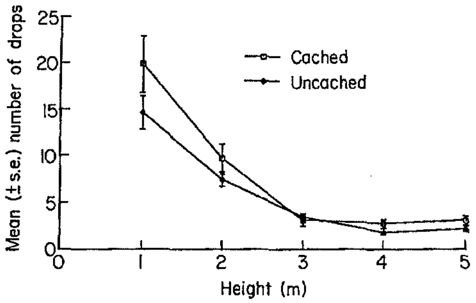

Figure 1. Number of drops required to break open cached and uncached mussels at a road dropping site. The mean number of drops required to break open a mussel is significantly correlated to dropping height for both cached (one-way ANOVA df = 4,95, $F = 16.2$, $P < 0.01$) and uncached (one-way ANOVA df = 4,95, $F = 12.8$, $P < 0.01$) mussels.

was no significant difference in the mean number of drops required to break open a cached or uncached mussel from the same height (two-tailed *t*-test, df = 38, ns).

DISCUSSION

The crows' behaviour while caching prey items obtained from the intertidal zone was similar to that previously described for the genus *Corvus*.[4,7,11,12] Crows use the same methods to cache intertidal prey items as they do for other prey species. James & Verbeek[9] showed that Northwestern Crows which hid clams singly and covered them with grass were more likely to avoid losing them to other crows than crows that cached clams in covered clumps or singly and uncovered. In the present study, observations showed that all prey items were cached singly and covered with grass. Thus crows attempted to minimize the risk of losing cached prey.

Over a 3-year period no other species at Lough Hyne were observed caching prey items and the remains of gull *Larus* sp. predation were deposited at readily identifiable middens on the edge of the lough and not on the hillside. Artificially cached mussels gaped, in an identical way to the bivalve molluscs recovered from the hillside, providing additional evidence that the latter were cached prey items. Prey items with hard shells or exoskeletons, and especially bivalve molluscs, were the only items recovered cached, although it is less likely that species without such a characteristic would be recorded by the method. However, James & Verbeek[9] also showed while bivalve molluscs were most favoured for caching, fish, insects and berries were also recorded. They attributed this to the capacity of bivalve molluscs to avoid rapid deterioration. In our study, no other prey species were observed being cached and thus any species not recorded are likely to be unimportant. Loss of flesh to scavenging arthropods, in the study by James & Verbeek,[9] increased dramatically after a mollusc had gaped which could take up to 2 days. Mussels at Lough Hyne could take up to 15 days to gape and this enables crows to cache them for a longer period. Six mussels cached by crows were still unrecovered after 21 days but over half (55%) were recovered within 3 days. The proportion of cached mussels recovered in the present study was at least 70% which compares favourably with 76% attained by Northwestern Crows.[9] The recovery efficiency of cached food by corvids is considered high[11] and is thought to be largely achieved by memory.[1]

Crows at Lough Hyne cached more prey items before low tide than after low tide, but were not observed to recover prey items until the tide had fully covered the beach. The tidal cycle at Lough Hyne is asymmetrical and rises twice as fast as it falls.[13] The time available for foraging within the intertidal zone after low tide is small compared to before low tide and crows appear to concentrate their foraging activity before low water. Cached mussels that are retrieved with closed valves require dropping to expose their flesh. Mussels recovered when the tide had submerged the beach dropping site were broken open on the road. The road is 10–15 m above the beach and there is no difference in the number of drops required to break open a cached mussel relative to an uncached mussel. Vertical flight by crows requires a large expenditure of energy[14] and crows therefore expend more energy dropping mussels retrieved from a cache than dropping them directly. Hooded crows at Lough Hyne do not cache only the largest individuals, as found by James & Verbeek,[10] for Northwestern crows, and are not therefore expected to achieve a net energy gain equivalent to mussels that are dropped immediately. A mussel that has gaped does not require dropping and thus less energy is needed to obtain the mussel flesh.

The ecological implications of food caching by *Corvus* are poorly understood.[1,11] The storage of high energy foods is considered adaptive in corvids of temperature and subarctic zones[11] and hard-shelled molluscs would appear to be an ideal storage food as they have relatively high energy content and are protected in a shell. This behaviour has been recently described for Magpies *Pica pica*[15] and is probably widespread by crows. Clearly such adaptive behaviour must play an important role in the ecology of coastal breeding corvids.

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