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Consumption and Caching of Food in the Northwestern Crow (*Corvus caurinus*)

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Foraging behavior can be divided into two distinct types. When "feeding," a forager ingests all the food it captures. When "provisioning," the resources are delivered to a mate, to a cache site, or to offspring. These foraging modes are distinct because the costs and benefits differ (Ydenberg et al. 1994). Unlike feeders, provisioners pay time and energy costs for delivery and travel to and from the foraging site, and only some of the food they collect is consumed. The remainder is delivered to others, or is stored for later consumption. Thus, provisioners share (or defer) the benefits of foraging, but bear all the costs. Due to these differences, the relative profitability of food items or feeding sites depends on the foraging context.

The Northwestern Crow (*Corvus caurinus*) exhibits a natural daily rhythm in foraging mode, feeding at high tide when food is less available, and provisioning food to cache sites at low tide (James and Verbeek 1983). We simultaneously presented crows with two experimental foraging sites (patches) offering different feeding rates. We predicted that when feeding at high tide, crows would prefer the patch with the higher feeding rate. However, the provisioning rates attainable from the patches were nearly identical, and we predicted that when provisioning at low tide, the crows would be indifferent between the two.

Methods.—The study was carried out during May and June of 1993, on Diana Island near the Bamfield Marine Station, British Columbia, Canada (125°11.5′W, 48°51′N). The two patches were planks of driftwood placed 9 m apart high up on the beach so that they were accessible at all tides. We placed 120 empty mussel valves in a regular array at a density of about 25 valves/m² in each patch. Patch type A had one piece of Purina Puppy Chow hidden under each valve, while patch type B had three pieces under one-third of the valves (chosen randomly). Crows foraged by turning each valve over and picking up the puppy chow pieces one by one. Due to the different dispersion of Puppy Chow pieces under the mussel valves, crows could find food slightly faster in patch A (1 s of search per piece) than in patch B (1.25 s of search per piece).

Crows ingested these pieces when feeding, but when provisioning held them in the beak and throat, transporting them into the nearby forest where the pieces were cached.

We calculated the feeding rates attainable in the two patch types as the net energy gain per piece (energy per piece minus the energy costs of search and handling) divided by the time required to search for (1.0 s in patch A and 1.25 s in patch B) and handle (0.5 s) each piece. We estimated the cost of search as 14.4 W (4 × BMR, using 3.6 W as BMR; see Richardson and Verbeek 1986), and the cost of handling as 7.2 W (2 × BMR). The advertised energy content of Purina Puppy Chow is 8 kJ per piece. These calculations revealed that crows could feed at a rate of 5.3 W in patch A, and 4.3 W in patch B.

Provisioning crows gathered a load of (almost always) three pieces and made a trip to the forest to cache the pieces before returning to collect another load. We calculated the provisioning rate attainable from each of the patch types as the net energy gain per provisioning trip: energy in three pieces minus the energy costs of search (3 s in patch A and 4 s in patch B at 14.4 W), handling (1.5 s at 7.2 W) and delivery (30 s at 9 × BMR, or 32 W), divided by the time to collect and store each load. The long duration of the caching trip (30 s) relative to the load collection time so diluted the impact of the slight differences in collection time between the patches that the attainable provisioning rates were effectively equal at 0.65 kW, differing by less than 3%.

A group of 9 to 12 crows, very likely the same individuals, frequented the beach and quickly learned the experimental procedure, often waiting nearby for trials to begin. A trial was conducted by preparing both patches and, from a viewing site 50 m away, counting at 5-s intervals the number of crows foraging in each patch, until one of the patches was exhausted. Individual crows often moved between patches during trials. The average number of crows was scored for both patches for each trial. Each trial took between 15 and 30 min to complete and several

TABLE 1. Mean (±SE) number of crows in each patch type when provisioning (low tide) and feeding (high tide).

| No. crows at | No. trials | Patch type | | t^a | Total[b] |
		A	B		
High tide (feeding)	63	8.8 ± 1.4	0.9 ± 1.2	28.0**	9.7 ± 0.5
Low tide (provisioning)	37	4.3 ± 1.2	5.0 ± 1.2	1.94[ns]	9.3 ± 0.8

[a] Paired t-test matching patch A and B within trials. **, $P < 0.01$; [ns], $P > 0.05$.
[b] t-test comparing total number of crows at low (provisioning) and high tide (feeding) trials, $t = 2.85$, $P < 0.01$.

could be completed per tidal cycle. Patch types alternated between the two planks in successive trials, and totals of 63 high-tide (feeding) and 37 low-tide (provisioning) trials were conducted. Crows always cached the pieces at low tide and consumed them (fed) at high tide. Statistics follow Bruning and Kintz (1968).

Results and discussion.—Table 1 shows a small but significant difference between high and low tide in the total number of crows foraging at the patches. However, this difference was too small to account for the different allocation of crows between the patch types at high and low tide. As predicted, most of the crows were in patch type A while feeding, but were evenly distributed between the two patch types when provisioning.

The results demonstrate that foraging context is important. This may have broad significance for the study of avian diets. For example, all altricial bird species show a sudden switch from feeding to provisioning during the breeding season when they must begin provisioning their offspring. In some species, courtship feeding of the female by the male occurs, which also is a form of provisioning. Changes in diet with the onset of breeding or hatching have been documented for a variety of species (Austin 1976, Custer and Pitelka 1978, Conner 1981, Jamieson et al. 1982, Franzreb 1983, Robinson 1986, Annett 1987, Houston 1987, Petit et al. 1990, Sakai and Noon 1990). The explanation most commonly given is that there exists a parallel change in food availability (but see Robinson 1986), though this has rarely been measured, and has never been tested rigorously. Our results show that the change in foraging costs and benefits associated with the change from feeding to provisioning provides a good explanation for the change we observed in the distribution of foragers across patches, and by extension may also explain the changes in diet observed in the above studies.

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