

FOOD CHOICES BY NORTHWESTERN CROWS: EXPERIMENTS WITH CAPTIVE, FREE-RANGING AND HAND-RAISED BIRDS¹

MARY F. WILLSON AND TALLCHIEF A. COMET

Forestry Sciences Laboratory, 2770 Sherwood Lane, Juneau, AK 99801-8545

Abstract. Captive adult Northwestern Crows (*Corvus caurinus*), foraging individually, were selective of native Alaskan fruits. Most individuals had color preferences, commonly preferring red, blue, or green over yellow. They often favored high-lipid artificial fruits over low-lipid, but only sometimes favored artificial fruits with high levels of corn syrup or sucrose over those with low sugar levels. However, decreased accessibility of the favored fruits generally eliminated the preference for high lipid or high sugar, although accessibility did not alter preferences in parallel experiments with domestic cherries. Artificial fruits with high seed loads were not avoided. In all of the above experiments, individual variation was conspicuous. Crows showed no evidence of learning foliar cues for fruit selection.

Hand-raised crows did not prefer the color of the food upon which they were raised. They exhibited extensive individual variation in preferences for color, lipid and sugar content. Free-ranging crows often foraged in groups, lacked the experience of the captive crows with the visual cues available to identify nutrient levels in the experimental fruits, and commonly did not make the same choices collectively as the captive crows. We interpret the extensive variation among individuals, the flexibility of choice, and the difficulty of assessing nutrient levels in conspecific natural fruits as evidence that selection by Northwestern Crows on the fruit traits examined is probably weak and variable.

Key words: Northwestern Crows; *Corvus caurinus*; food choices; food preferences; frugivory; fruit traits.

INTRODUCTION

If the characteristics of fleshy fruits have evolved in response to selection pressures from frugivores, it should be possible to demonstrate that frugivores choose fruits on the basis of specific traits. Such choices should be strong (not easily changed) and consistent to make a good case for present-day selection pressures. Geographic and phylogenetic patterns of fruit morphology in closely related taxa suggest that at least some fruit traits may not reflect current selection (Herrera 1986, 1988, 1992; Jordano 1987, 1989), although other traits, such as color, are not necessarily included in this assessment (Willson and Whelan 1990).

The series of experiments reported here represents an expansion of our previous work with food choices of frugivores (Willson et al. 1990). Here we examine the food choices of an additional species of frugivore, the Northwestern Crow (*Corvus caurinus*), with respect to several fruit traits. Specifically, several questions are asked: (1) Do crows prefer certain kinds of nat-

ural fruits? Choices among equally available natural fruits may yield some indication of the traits used by the frugivores in making choices. (2) Do crows exhibit a preference for particular colors of artificial fruits? Do crows prefer one color morph of species with polymorphic fruits? Color preferences might be one source of selection on fruit color (Willson and Whelan 1990, Willson et al. 1990). (3) Do crows prefer artificial fruits that contain high levels of basic nutrients, such as sugar or lipid? (4) How do small changes in food accessibility alter the choices seen in #3? Changes in accessibility are expected to alter preferences (Moermond and Denslow 1983, Denslow and Moermond 1982, Levey et al. 1984). If slight changes in access alter preference rankings, the strength of that preference can be judged to be weak. (5) Do crows exhibit preferences for artificial fruits that have a small load of seeds? If yield of fruit pulp per bite is maximized, preference for small seed loads may select for pulpy fruits. (6) Do crows learn to use leaves to locate or identify a preferred fruit? When fruits are scarce or when two species of fruit closely resemble each other, leaves (or other signals) might provide an ancillary signal for fruit identification and location. (7) What food choices are made by hand-

¹ Received 15 October 1992. Accepted 11 March 1993.

reared juveniles that have little early experience with food choices made by their parents? Do they prefer the colors of the foods fed to them as nestlings? Do they exhibit the same preferences as adults captured from the wild? (8) Do captive crows exhibit choices similar to free-ranging crows? If the results from aviary birds are to be extended to the natural situation, one must show that the experimental outcomes are similar.

METHODS

Crows. Northwestern Crows were chosen for these experiments because they are partially frugivorous, readily available in our area, and easy to maintain in captivity. North American species of *Corvus* are often frugivorous to some degree. The American Crow (*C. brachyrhynchus*) eats many kinds of fruits, often in large quantities (Bent 1964; Kalmbach 1918, 1920), as does the so-called Fish Crow (*C. ossifragus*) (Barrows 1889, Bent 1964, Martin et al. 1951). Both the Chihuahuan Raven (*C. cryptoleucus*) (Bent 1964, Martin et al. 1951) and the Common Raven (*C. corax*) (Bent 1964, our observations) eat at least some fruit. The Hawaiian Crow (*C. hawaiiensis*) is very frugivorous (Sakai et al. 1986, Sakai and Carpenter 1990). The Northwestern Crow, sometimes considered to be a race of the American Crow, is best known as an intertidal forager. However, in southeastern Alaska, Northwestern Crows eat many fruits of the introduced European mountain ash (*Sorbus aucuparia*) (our observations), as well as elderberries (*Sambucus racemosa*) and salmonberries (*Rubus spectabilis*) (Armstrong 1990). Northwestern Crows also readily accepted and ate or cached the domestic grapes (*Vitis* sp.) we used as bait in trapping operations.

Feeding experiments—captive adult crows. We trapped crows for the aviary experiments at Lena Point and Eagle Beach near Juneau. After pre-baiting with bread and grapes, we used a dropnet trap to capture the crows in late April, 1990 and 1991. Although the birds were wary of the trap, they visited it repeatedly, and all experimental birds were captured within a few days. Separate cohorts of birds were tested in the two years. All captives were released at the end of the experiments in each year.

Captive crows were maintained in an outdoor aviary in Juneau. Each bird was housed separately in a cage 2 m × 2 m × 2 m, with a long perch along the back wall. The crows were main-

tained on a diet of raw fish, Science Diet® kitten kibble, hard-boiled egg, domestic fruits (principally grapes, banana, cherries, raspberries), bread, and banana-agar mash (Denslow et al. 1987). The birds had auditory and visual contact with each other. As crows commonly live and forage in flocks, visual contact for the experimental birds was appropriate. If this led to some choices by imitation of neighbors, that may be normal for flock-feeding birds. However, adjacent birds were often out of phase with each other in the sequence of experiments, and the results show that individual variation was considerable. Several weeks elapsed between the time of capture and the beginning of the experiments, giving the birds time to adjust to captive conditions.

Most experiments were conducted with hungry birds, in order to obtain results expeditiously. Their maintenance food was removed at dusk the previous evening, so that the first food available on the morning of the experiment was the experimental food. Experiments usually began about 08:00 hr and often lasted until early or mid-afternoon, when the maintenance diet was renewed.

The behavior of the captive crows in most experiments was observed from a movable blind, built of plywood and one-way glass, located about 2–4 m from the individuals under observation. The observer set up the experiment, entered the blind, and recorded data. The observer was often able to experiment with several birds simultaneously. The participating birds often finished each set of trials at different rates, so that adjacent birds might be involved in different experiments; this is why only the starting dates are given in the summary table (Table 1). Birds varied greatly in their willingness to participate in experiments. A few refused altogether and were released, and others refused occasionally (accounting for the variable sample sizes in the summary table [Table 1]).

Experiments with real fruits.—Experiments with native fruits used an array of fruits chosen solely on the basis of availability. These experiments were “cafeteria”-style, in which a variety of fruits was presented simultaneously. Experiments with fresh native fruits could be conducted only when those fruits ripened, so the cafeteria experiments were run in late summer. The array of fruits tested depended on availability, which differed in 1990 and 1991. Fruit colors are indicated in parentheses, unless obvious from the

TABLE 1. Summary of choice experiments with captive crows: chronological order, numbers of birds for which data were obtained, number of trials per bird, principal variables and cues, location of trial within the cage, and purpose. Location refers to placement of the experimental food within the cage: many trials were run with the food dishes on the floor, but some were run on perches inserted into the sides of the cage, and others on a pedestal in the center of the cage (see text). Different cohorts of birds were used in 1990 (experiments 1–30) and 1991 (experiments 31–41). Number of birds varied among trials because some birds sometimes refused to eat fruit; where two numbers are given, the first shows the number of birds completing all trials and the number in parentheses includes birds completing only some of the trials. The number of trials for color preferences is given as 24; this refers to four trials for each of six pairwise color combinations (four colors, taken two at a time). Nutrient concentrations are given as multiples of those in the banana-mash recipe of Denslow et al. (1987). For lipids, the actual concentrations were determined to be about 2% (dry mass) for the basic recipe, and about 11% for “5 × lipid” (Palmer Research Center, Palmer, AK); comparable figures for sugar levels were not determined. For experiments in which nutrients or seed load were the experimental variable and the cue was a slight difference in intensity of hue, the association between cue and variable state is indicated in the cue column (e.g., dk = hi or dark hue indicated high level; lt = hi or light hue indicated high level). For some sugar trials, c.s. = corn syrup. When cues were reversed in succeeding experiments, this is indicated in the table; same indicates that the association was the same as in the preceding experiment. The count method was used in all experiments except where mass method is indicated (see Methods).

No.	Date begun	No. birds; trials/bird	Variable	Cues	Location	Purpose
1	1990 22 May	9; 24 (6 color pairs)	color	color	floor	color pref., transitivity
2	27 May	6(8); 6	lipid (10 ×)	hue (R), lt = hi; dish color	floor	lipid pref.
3	27 May	5(7); 4	cherry	cherry	floor	cherry pref.
4	1 June	9; 4	lipid (8 ×)	hue (R), lt = hi; dish color	floor	lipid pref., lower conc.
5	1 June	8(9); 4	lipid (8 ×)	hue same; dish color reversed	floor	lipid pref., reversed back- ground
6	5 June	4(6); 4	sugar (7 × corn syrup)	hue (B), dk = hi; dish color	floor	sugar (c.s.) pref.
7	5 June	8; 4	sugar (5 × corn syrup)	same	floor	sugar (c.s.) pref., lower conc.
	5 June	9; 2	cherry on leaf	cherry and leaf	floor	training
	5 June	9; 6–16	cherry under leaf	leaf	floor	training
8	8 June	8; 9	cherry under leaf	leaf	floor	use of leaf cues
9	12 June	9; 4	lipid (5 ×)	hue (R), lt = hi; dish color	floor	lipid pref., lower conc.
	13 June	9; 2	lipid (5 ×)	hue same; dish color reversed	floor	training
10	13 June	9; 4	lipid (5 ×)	same	floor	lipid pref., background reversed
11	14 June	5; 4	lipid (5 ×)	hue (R), lt = hi	perch, long reach	effect of accessibility on pref.
12	15 June	8(9); 4	lipid (5 ×)	same	floor	lipid pref., single cue; new baseline
13	15 June	7; 4	lipid (5 ×)	same	perch, short reach	effect of accessibility on pref.
14	18 June	8(9); 4	lipid (5 ×)	same	floor	lipid pref., new baseline
15	18 June	7; 6	lipid (5 ×)	same	perches	accessibility: long reach, cross-cage
16	19 June	9; 4	cherries	cherry	perches	accessibility: long reach, cross-cage
	20 June	8; 2	lipid (2 ×)	hue (R), lt = hi	floor	training
17	20 June	8; 4	lipid (2 ×)	same	floor	lipid pref., lower conc.
	21 June	7; 2	lipid (8 ×)	same	floor	training
18	21 June	7; 4	lipid (8 ×)	same	floor	lipid pref., new baseline
19	22 June	7; 4	lipid (8 ×)	same	perches	accessibility: long reach, cross-cage; high lipid conc.

TABLE 1. Continued.

No.	Date begun	No. birds; trials/bird	Variable	Cues	Location	Purpose
20	25 June	8(9); 4	sugar (5 × sucr.)	same	perch, one dish	sucrose pref.
21	26 June	6(7); 6	Rainier cherry	color	perch, one dish	color pref.
	27 June	7; 8	lipid (5 ×) vs. sugar (5 × c.s.)	hue (R), dk = lipid	perch, one dish	training
22	28 June	7; 4	lipid (5 ×) vs. sugar (5 × c.s.)	same	perch, one dish	lipid vs. corn syrup pref.
23	28 June	6; 2-6	salmon berry morphs	color	perch, one dish	morph pref.
	29 June	7; 2	sugar (5 × sucr.)	hue (R), lt = hi	floor, 2 dishes	training
24	29 June	7; 4	sugar (5 × sucr.)	same	floor, 2 dishes	sucrose pref.
	3 July	7; 7-8	lipid (5 ×) vs. sucrose (5 ×)	hue (R), dk = lipid	floor, 2 dishes	training
25	5 July	7; 4	lipid (5 ×) vs. sucrose (5 ×)	same	floor, 2 dishes	lipid vs. sucrose pref.
	6 July	7; 2-8	lipid (5 ×)	reversed hue, dk = hi	floor	training
26	6 July	7; 4	lipid (5 ×)	same	floor	effect of reversed cue
	30 July	7; 9-13	lipid (5 ×)	position (front/back)	perch	training
27	31 July	7; 4	lipid (5 ×)	same	perch	accessibility
	1 Aug	7; 18-22	lipid (5 ×)	position (rt/left)	pedestal	training
28	3 Aug	7; 4	lipid (5 ×)	same	pedestal	effect of position cue
29	7 Aug	7; 8	native fruits	fruits	cafeteria on floor	fruit prefs.
30	8 Aug	7; 8	native fruits	fruits	cafeteria on floor	fruit prefs., top choice missing
31	1991 31 May	8; 24 (6 color pairs)	color	color	pedestal	color prefs., transitivity
32	14 June*	7; 4	lipid (3 ×)	hue (R), dk = hi	pedestal	lipid pref.
33	20 June*	6; 4	lipid (3 ×)	position (rt/left)	pedestal	effect of position cue
34	25 June	6; 4	lipid (3 ×)	same	pedestal	effect of position cue mass method
35	1 July*	7; 4	glucose (3 ×)	hue (R), dk = hi	pedestal	glucose pref.
36	5 July*	7; 4	glucose (3 ×)	position (rt/left)	pedestal	effect of position cue
37	5 July	7; 4	glucose (3 ×)	same	pedestal	effect of position cue mass method
38	19 July	6; 4	salmonberry morphs	color morph	pedestal	morph pref.
39	25 July*	6; 4	glucose	hue (R), dk = hi	pedestal	accessibility, short reach
40	29 July	7; 4	native fruits	fruits	cafeteria on floor	fruit prefs.
41	8 Aug*	6; 4	seed load	hue (R), lt = seedy	pedestal	seed-load pref.

* Each of these experiments was preceded by one to several days of training, in which the birds were allowed to feed ad libitum on the test food in the test arrangement.

common name. In the first year, we used early blueberry (*Vaccinium ovalifolium*), devil's club (*Oplopanax horridum*; red), crowberry (*Empetrum nigrum*; black), elderberry (*Sambucus racemosa*; red), cloudberry (*Rubus chamaemorus*; yellow), and nagoon berry (*R. arcticus*; red). In the second year, we used early blueberry, red

huckleberry (*Vaccinium parvifolium*), devil's club, elderberry, salmonberry (*Rubus spectabilis*) of two color morphs (red and gold), and clasping twisted-stalk (*Streptopus amplexifolius*; red to black). Roughly equal volumes of fruits were displayed in petri dishes in a circular array on the floor of the cage, in haphazard order, and the array was

rotated between trials. Preference was defined as the fruit type that was first to be consumed completely.

Several fleshy-fruited species are polymorphic for fruit color (Willson 1986, unpublished), and this variation provides a tool for examining the possible role of color preferences in maintaining the polymorphism. We examined crow preferences for color morphs, recognizing that the color polymorphism may have associated taste/nutrient/digestibility differences as well. We used natural fruits of *Rubus spectabilis*, which occur in red and gold forms. Both the red and the gold morphs are common in southeastern Alaska, but red appears to be somewhat more abundant. In addition, fresh "Rainier" cherries, with a red blush on one side of a yellow fruit, were used to augment experiments on native polymorphic fruits. The cherries were cut in half, producing a red and a yellow piece to simulate a red and a yellow morph, and the two halves were presented to the birds.

We also established the crows' choice between dark red, sweet (dessert) cherries and light red, tart (pie) cherries, using frozen, pitted domestic cherries. Preferences from this experiment provided a useful tool for subsequent experiments on cue learning and a pointed contrast with the effects of accessibility in the lipid trials (see Results).

We examined the possibility that crows might use foliar cues to locate favored foods, using domestic cherries with alder (*Alnus sitchensis*) and cottonwood (*Populus trichocarpa*) leaves. Neither alder nor cottonwood produces fleshy fruits; they were selected for large leaf size, availability, and lack of natural association with fleshy fruits. Alder leaves have strong veins and toothed margins; cottonwood leaves are smooth on surface and edge. Details of the training procedure for this experiment are found in the Results.

Experiments with artificial fruits.—Pairwise experiments on preferences for color, nutrient levels, and seed load were conducted with artificial fruits, made from banana mash. In 1990, the artificial fruits were cubes of mash about 0.8–1.0 cm on a side. In 1991, we used pellet molds (see Levey and Grajal 1991) to make spherical "fruits" about 1 cm in diameter. These fruits were dyed red, blue, yellow, or green, using commercial food coloring: Munsell colors approximately 7.5R 3/12, 10B 3/10, 5Y 8/14, 2.5G 4/10, respectively. Food coloring is not without flavor,

but we ignored this possible confounding variable on the presumption that other flavors in the food would mask the flavor of the coloring material. The intensity of the hues was kept as consistent as possible among trials, but all colors darkened upon exposure to air. Red and blue represent the common mature fruit colors of native fruits in southeastern Alaska, whereas yellow and especially green are rare. The color-choice trials presented all possible pairs of the four colors, in randomized order. In these and in other trials in which foods were presented in two dishes, the right/left position of the two dishes was alternated between trials; the only exceptions were trials in which right/left position itself was the foraging cue.

For most experiments we employed the "count" method, presenting four fruits of each kind in pairwise experiments, then watching and recording until half of the total had been taken. This method allowed the experiments to proceed relatively quickly, because the removal of half of a small number of fruits usually occurred quite rapidly. However, under these conditions, one could argue that a hungry bird might "intend" to eat all of the presented fruits and the order of its taking the fruits might actually be trivial (see also Peterson and Renaud 1989). We therefore initiated a second series of experiments, in late summer 1990 and in 1991, using a "mass method." We placed a known and equal mass of food in each of the two experimental dishes presented to each bird, in amounts sufficient that a crow was unlikely to consume all of it in just a few minutes (i.e., 20–40 g). The experimental dishes were left in the cage (unobserved) until about half of the food was removed, and the remaining food was weighed. The difference represents the amount eaten (plus a small amount of evaporation). Because the observer was not continually present, and we had no way of knowing when exactly half was reached, the actual amount eaten by each bird varied. The "mass method" trials often took several hours per trial, because the birds ate more. However, this method should reduce the potential problem of a hungry bird simply eating everything in sight in no particular order. Because evaporative losses were both minor and similar for the foods given to any one bird, we analyzed the data simply as the amount eaten, without the more sophisticated approach of Peterson and Renaud (1989).

Before the birds were tested on nutrient con-

tent and seed load, they were given experience ("training") with the cues associated with the experimental variable (Table 1). Each bird was given opportunities to sample the experimental food and, potentially, to learn the associated cue before the preference tests began. In most cases, training sessions used the experimental set-up, but sometimes (when training continued for several days) the training food was presented on the floor along with the maintenance diet (which was, however, removed if birds failed to eat the training food).

The lipid used to create artificial fruits of differing lipid concentration was commercially available corn oil (Mazola®). Experimental concentrations are given here as multiples of the level in the banana-mash recipe (e.g., $5 \times$ lipid = five times the recipe level). We began the sugar trials in 1990 with white table sugar (sucrose) and corn syrup (glucose and fructose). In 1991, we used pure glucose. For the experiments in which the crows were given a choice between fruits of differing seediness, we made spherical artificial fruits enclosing one (low seed load) or six (high seed load) seeds of *Rubus spectabilis*.

Placement of the experimental food dishes within the cage varied. We began by placing the dishes on the floor, where the maintenance diet was kept. Some trials were conducted on experimental perches inserted into both sides of the cage at about 1 m above the floor. These perches were used to examine the effects of accessibility on preferences and for some sugar trials in which a single food dish was used, with foods arranged alternately around the edge of the dish. The perches could not be used for examining position (right/left) cues, however, because many of the crows showed a marked preference for feeding on one side of the cage (cage-sidedness) or approaching the feeding perch from a particular angle. Position-cue experiments, plus most trials in 1991, were run on a pedestal (about 0.5 m tall) placed in the center of the cage; it consisted of a perch just wide enough for the bird to land on, with two dishes attached to the front. This arrangement reduced the problems of cage-sidedness and increased our ability to observe the crow's behavior.

We performed several variations of the accessibility experiments. One version required the crows to make a long downward reach (~13 cm) for the preferred food. A second version required a short downward reach (~6 cm in 1990, 4 cm

in 1991). In both cases, the food was placed in two small petri dishes, one at perch level, the other at the stated distance below and slightly offset, so it was not blocked by the upper dish. A third version presented a less-favored food in a dish in front of the perch ("front" determined by the direction used by the approaching bird) and a favored food behind the perch, both at equal distances and level with the perch. This arrangement required the bird to reach behind or turn around to obtain the favored food (or to approach from another angle, which virtually never happened). A final version provided two food dishes, one above the other (13 cm), on each side of the cage, thus providing two different types of decreased accessibility—a downward reach and a cross-cage flight. In these cross-cage experiments, the presumably favored food was placed in the upper dish on one side of the cage and the lower dish on the other, while the less favored food was placed in the other two dishes; the location of the favored food was alternated with that of the less favored food in successive trials. Thus, in any one trial, food Q would be found in an easily reached position on one side of the cage, but in a less easily reached position on the other side. If reduced accessibility altered the expression of food preference, the birds would be predicted to take first the food items (a) on the same side of the cage, from both upper and lower dishes or (b) in the upper dishes on either side of the cage. We expected that cross-cage flights would require more effort than reaching down, and thus expected option *a* to be more common than option *b*.

The order of the experiments with captive adults is presented in Table 1: Expts 1–30 for 1990, Expts 31–41 for 1991, using different sets of birds in each year. For each experiment we show the principal variable of interest, the cues associated with that variable, the number of birds participating in the experiment and the number of experimental trials per bird, the location of the experiment within the cage, a brief indication of the chief purpose of the experiment, and any preceding training periods. It is important to know the order of the experiments, because experience might alter the outcome of later experiments in ways that were not part of the experimental design. The order of the experiments was determined by several considerations. We did the experiments with color preference first, partly because that was one of our principal interests

(continuing earlier work), and partly to ascertain which colors to use as cues in subsequent experiments. Lipid trials were initiated next, because we wished to examine a published suggestion that birds may prefer high-lipid fruits (Stiles 1980). However, the order of the lipid experiments reflects successive adjustments of cues and of lipid concentration: we began with two cues (see Table 1), in hopes of providing a clear opportunity for the crows to learn which food was which, and later reduced this to one cue. At first, we used large differences in lipid concentrations, to maximize the contrast. The lipid concentration was reduced successively, partly to reduce the texture difference caused by large amounts of lipid, and partly to see if choices became less clear at less contrasting concentrations. Experiments with domestic cherries were interspersed, to provide some variety for both crows and experimenters. Sugar experiments came later in the sequence, because they were more exploratory in nature, although a general expectation was that the birds would favor high levels of sugar. Only after the experiments were begun did we learn of the work of Martínez del Rio and colleagues (refs. below) on sugar assimilation by birds. The small experiment with seed loads in 1991 was again exploratory, to test the hypothesis that foragers should prefer to feed on fruits with low seed loads, to maximize pulp intake and/or to minimize the load of indigestible ballast.

Feeding experiments—hand-raised crows. The hand-reared crows were taken from nests in a colony at Eagle Beach, north of Juneau, in June 1990. No more than two nestlings were taken from each nest. All nestlings were taken before the eyes were open, although eye-slits were present in some. They were segregated into three experimental groups, to be reared on foods of three different colors. Their diet was similar to that of captive adults, except that the banana mash was augmented with chick starter (poultry chow) and cooked chicken was also provided. One group of nestlings was fed only red foods (dyed with food coloring), one on yellow foods (dyed), and one on natural-colored foods, until they were sufficiently able to feed themselves.

When the eight hand-raised crows were able to feed themselves readily, we began a color preference experiment (27 Aug. 1990; 24 pairwise trials/bird). This was followed by a series of 30 trials for lipid preference, divided into three sets

of 10 each, in order to examine trends (begun on 29 Aug., 10× lipid, red fruits, count method; right/left positions were not alternated in this experiment—instead, different birds had high lipid on the right or on the left). On 31 Aug., we examined lipid preferences by the mass method. On 7 Sept., the juveniles were trained (six sessions) on 10×:1× corn syrup, before four test trials on this contrast. On 17 Sept., corn-syrup preferences were examined by the mass method.

Feeding experiments—free-ranging crows. Feeding experiments with free-ranging crows were conducted near five different colonies along the coast near Juneau. In early September 1990, a flock in downtown Juneau was used. In 1991, we used sites near four breeding colonies. The Eagle Beach site is 47 km northwest of downtown Juneau, Lena Point is 29 km northwest of downtown, Sheep Creek is 5 km southeast of town, and Sandy Beach is 3 km south of downtown, across the Gastineau Channel from Sheep Creek. All 1991 experiments were run during late May to late July, when the crows abandoned their breeding colonies.

Experiments with free-ranging crows were set up on the ground or on picnic tables. Because wild crows fed rapidly and in groups, the count method was difficult to use, and therefore most experiments with artificial fruits used the mass method. The cafeteria experiment with native fruits was set up like that for aviary birds, but the color preference experiments presented all four colors simultaneously rather than pairwise. Lipid levels differed by 2× in 1991 and 10× in 1990 (only 1 flock); glucose levels differed by 3×. For the seed-load experiments, one small, black, domestic sunflower seed was inserted into artificial fruit pellets to make fruits with a seed load, to be tested against those with no seed load. These seeds were initially not visible to the crows, but sometimes the feeding activity of the birds would move the fruits and expose the insertion point and a glimpse of the seed inside.

Statistical methods. Statistical tests include χ^2 and binomial tests. We used the conventional criterion of $P < 0.05$ to determine statistical significance (indicated by * in text and tables). In addition, a somewhat unconventional level of marginal significance was used for χ^2 tests ($0.05 < P < 0.15$), in order to include a slightly broader spectrum of tendencies to favor one kind of fruit; by this criterion, a ratio of 11:5 is marginally

significant by χ^2 test. Marginal significance is indicated by (*). An alternative approach would have been to use one-tailed Chi-square tests for cases in which there was an a priori prediction. This would make an 11:5 ratio marginally significant by conventional standards (i.e., $P \leq 0.10$). The outcome of these two procedures is similar in detecting marginal significance, but the two-tailed test, with a somewhat unconventional criterion, allowed the discernment of trends in opposition to the prediction.

Data from the mass-method experiments were analyzed by analysis of variance (ANOVA) (on arcsine transformed proportions). Because the structure of the data did not allow simultaneous testing of repeated measure (trials) and both factors of interest (birds or flocks and fruit traits), all data were first run in a separate repeated-measures ANOVA. The repeated-measures analysis showed that there were no significant effects of repeated trials with the same bird or flock, except for Experiment 34. For this exception, the effect of trial was erratic, showing no evident temporal pattern, and we then treated the trials as effectively independent measures in a two-way mixed model ANOVA. Because the data were thus used twice, a Bonferroni adjusted criterion of significance ($P \leq 0.025$) was used. The results for the differences in fruit traits were very similar in the two-way ANOVA and the more conservative repeated-measures ANOVA: all significant P values were < 0.02 for both kinds of tests; for economy of space, only results of the two-way ANOVA are reported in the text.

For the two-way ANOVAs, the procedure for the mixed model normally requires that the mean square of the fixed effect be divided by the mean square of the interaction term, when the interaction is significant. However, in some cases, when the effect of the tested factor is clear despite the interaction, it is appropriate to use the mean square of the error term in the denominator (Sokal and Rohlf 1981). This procedure was used when the direction of the choice was consistent among birds, and the significance of the interaction was due to differences among birds in the magnitude of the preference. Use of this procedure is indicated in the Results by the larger number of degrees of freedom in the denominator for the F value of the fixed effect. When we report that crows "favored" or "preferred" one food type over another, such differences are

at least marginally significant, and the level of significance is indicated in tables or text.

The results are presented in an order that matches that of the questions in the Introduction.

RESULTS

Cafeteria experiments. Offered a choice among several natural fruits, seven birds in 1990 usually preferred early blueberry to the remaining five kinds of fruit (Expt 29; $\chi^2 = 152$, $P \ll 0.01$; Table 2). In the absence of this blueberry (Expt 30), three of the seven birds usually preferred devil's club, one preferred devil's club and nagoon berries equally, one preferred nagoons, and two selected three or four fruit types about equally. Overall, in Expt 30, devil's club was most preferred and crowberry the least preferred ($\chi^2 = 22.9$, $P < 0.01$).

The preferences were very different for the 1991 cohort of birds (Expt 40; Table 2). Early blueberry was preferred in only a few trials, and devil's club was never favored. Three birds usually preferred red salmonberry, two chose twisted-stalk, one usually favored gold salmonberry, and one chose red salmonberry and twisted-stalk equally. In total, red salmonberry and twisted-stalk were most often preferred ($\chi^2 = 17.4$, $P < 0.01$).

The principal interpretation of these results is that the crows exhibited considerable individual variation in the fruits favored. In addition, not surprisingly, apparent preferences shifted when the array of fruit species changed. Although all birds picked early blueberry over other fruits in the first year, birds in the second year ranked the blueberry much lower. Both elderberry and devil's club were sometimes favored by some birds in 1990, but by none in 1991, when salmonberry and twisted-stalk were favored.

Color experiments. Crows exhibited considerable individual variation in color preferences in both years (Expt 1—1990, Expt 31—1991; Table 3). In 1990, all nine birds preferred red and blue to green and yellow, but three (#2, 5, 6) preferred red to blue, one (#7) preferred blue to red, and the remainder were indifferent. Green was rejected (least preferred in all pairwise combinations) by five birds (#2, 3, 4, 8, 10) and yellow by two (#6, 7); one bird showed no preference between these two hues. Eight of nine birds made transitive choices. Collectively, the birds ranked the four colors as follows: R > B > Y > G.

TABLE 2. Cafeteria experiments with captive North-western Crows. Entries in the table are the number of trials in which the indicated species was the first fruit to be completely consumed. There were eight trials/bird in 1990, and four in 1991. In the second experiment in 1990, the fruit most favored in the first experiment (early blueberry) was not presented to the birds. Only species that were preferred by at least one bird are included in the table. Chi-square tests on totals (see text); sample sizes too small for tests on individual birds.

	Bird	Early Blue- berry	Elder- berry	Nagoon	Devil's club	Crow- berry
1990 A						
Expt 29	2	6	2			
	4	8				
	6	7	1			
	7	7		1		
	8	8				
	9	6			2	
	10	6			2	
Total		48	3	1	4	
1990 B						
Expt 30	2	—	2	1	5	
	4	—	2	3	1	2
	6	—	3	2	3	
	7	—	2	1	5	
	8	—	1	1	6	
	9	—		4	4	
	10	—		6	2	
Total			10	18	26	2
1991						
Expt 40	1	2		2		
	3			3	1	
	4			3		1
	5		2	1	1	
	6	3		1		
	7	3		1		
	8	3				1
Total		11	2	11	2	2

These results seem to suggest a general tendency to favor red or blue and reject green or yellow.

However, in 1991, the choices were far less clear. Most birds (5 of 8) made intransitive choices. Three (#2, 3, 4) preferred green to at least two other hues and three (#1, 7, 8) chose green equally to red and blue. Four birds tended to reject yellow. Intransitivity of choices and individual variation make it impossible to rank the colors for all birds collectively.

In 1990, crows were given a choice of red or

gold fruits of salmonberry (Expt 23), and collectively showed no tendency to favor one over the other ($\chi^2 = 0.86, P = 0.35$, Table 4). The sample size for each bird was small, but one favored red, and two favored gold. In 1991, five of six birds preferred red to gold salmonberries in pairwise trials; one was indifferent (Expt 38). Collectively, the birds favored red ($\chi^2 = 45.4, P < 0.001$), although heterogeneity among individuals was also significant (Table 4). In 1991, the morphs of salmonberry were also included in the general cafeteria experiment, and a few individuals selected the red morph (see above). In addition, the birds collectively showed no preference for the red or yellow halves of "Rainier" cherries (Expt 21; $\chi^2 = 0.02, P > 0.85$), although one individual favored yellow (Table 4). Bird #7 in 1990 consistently and significantly favored gold salmonberry or yellow cherry morphs in both experiments.

Taken together, results from both years indicate a weak and variable tendency to avoid yellow, a weak and variable tendency to favor red or blue, and mixed responses to green. High frequencies of intransitivity and of variation among birds were evident. Crows showed indeterminate preferences between polymorphic fruits in 1990 but favored the red morph in 1991.

Cherry experiments. The crows uniformly and strongly preferred dark, sweet cherries over light, tart domestic cherries (Expt 3). Accessibility did not alter this preference (Expt 16; Table 5): All nine crows took the dark cherries first, usually the one in the upper dish and then the one in the lower dish, even though a cross-cage flight was required to do so. The light cherries were often not taken. Thus, the preference for dark cherries was relatively strong, remaining unchanged when accessibility was decreased.

Lipid experiments. Several experiments (Expts 2, 4, 5, 9, 10, 12, 14, 17, 18) with varied designs indicate that crows often, but not always, tend to favor high-lipid fruits (Table 6). In 1990, in a series of experiments using slight differences in color as a cue but with different lipid concentrations and experimental backgrounds (and equal accessibility), all showed a collective preference for high-lipid fruits, and most individuals tended to favor high-lipid fruits (but not always significantly). However, the heterogeneity χ^2 for all of these experiments was significant (Table 6), indicating significant differences in preferences among birds. Furthermore, the consistency of

TABLE 3. Color preferences of captive Northwestern Crows. The colors used were red (R), green (G), blue (B), and yellow (Y). For each pairwise combination of colors, the number of artificial fruits of each color taken by individual birds is shown. Where possible, the intransitive portion of the array is shown, in parentheses when contiguous portions are involved, and with five entries when the ends of the array are involved. A statistically significant difference ($P < 0.05$) is indicated by *; marginal significance ($0.05 < P < 0.15$) is indicated by (*) (see Methods).

Bird	R:G	R:Y	R:B	B:G	B:Y	G:Y	Transitivity
Expt 1							
2	15:0*	13:0*	16:0*	14:1*	14:0*	0:16*	R > B > Y > G
3	13:0*	14:1*	10:6	13:0*	15:0*	3:13*	R = B > Y > G
4	16:2*	14:2*	9:7	15:1*	16:1*	4:12*	R = B > Y > G
5	11:8	12:3*	14:3*	12:3*	14:1*	0:15*	intransitive; R > B > Y > G = R
6	14:2*	15:1*	14:0*	15:0*	16:0*	14:0*	R > B > G > Y
7	16:0*	15:1*	0:16*	14:0*	15:0*	13:1*	B > R > G > Y
8	15:0*	14:1*	6:8	15:0*	12:2*	1:16*	R = B > Y > G
9	14:2*	14:0*	9:7	15:0*	15:1*	5:9	R = B > Y = G
10	15:1*	14:0*	6:10	16:2*	14:0*	1:15*	R = B > Y > G
Total	129:15*	125:9*	84:57*	129:7*	131:5*	41:97*	
Het χ^2	n.s.	n.s.	*	n.s.	n.s.	*	
Expt 31							
1	11:5 (*)	10:6	11:5 (*)	10:6	4:12*	13:3*	intransitive
2	4:12*	16:0*	15:1*	4:12*	7:9	11:5 (*)	G > R > B = Y
3	4:12*	8:8	12:4*	4:12*	11:5 (*)	8:8	intransitive; G > (R, B, Y)
4	4:12*	16:0*	15:1*	4:12*	15:1*	12:4*	G > R > B > Y
5	16:0*	12:4*	11:5 (*)	11:5 (*)	0:16*	10:6	intransitive; R > (B, G, Y)
6	2:14*	15:1*	9:7	12:4*	15:1*	10:6	intransitive
7	9:7	16:0*	9:7	8:8	10:6	16:1*	intransitive; R = B = (G \geq Y)
8	16:0*	16:0*	16:0*	8:8	16:0*	15:1*	R > B = G > Y
Total	66:62 n.s.	109:19*	98:30*	61:67*	78:50*	95:34*	
Het χ^2	*	*	(*)	*	*	n.s.	

Heterogeneity χ^2 tests: Expt 1: all $df = 8$; R/G: $\chi^2 = 10.36, P > 0.20$; R/Y: $\chi^2 = 1.92, P > 0.10$; R/B: $\chi^2 = 50.72, P < 0.001$; B/G: $\chi^2 = 2.36, P > 0.98$; B/Y: $\chi^2 = 4.16, P > 0.90$; G/Y: $\chi^2 = 69.34, P < 0.001$; Expt 31: all $df = 7$; R/G: $\chi^2 = 55.38, P < 0.001$; R/Y: $\chi^2 = 18.03, P < 0.01$; R/B: $\chi^2 = 13.38, 0.05 < P < 0.10$; B/G: $\chi^2 = 18.97, P < 0.01$; B/Y: $\chi^2 = 57.88, P < 0.001$; G/Y: $\chi^2 = 11.14, P > 0.10$.

each bird differed during the series of experiments: Birds #4, 6, 7, and 9 generally preferred high lipid but reversed or lost their preference in one or two experiment(s). Bird #10 favored high lipid in five of nine experiments. Birds #3 and 8 favored high lipid in only a few experiments and had no significant preference (or, occasionally, a reversed preference) in the remainder. Bird #5 seldom exhibited a significant preference. Only one bird (#2) favored high lipid consistently (but not always significantly).

In a series of experiments in which lipid concentration in high-lipid fruits diminished from 8x to 2x (Expts 4 to 17 in Table 6), only three birds (#3, 4, 6) showed a decreased preference for high lipid. However, no strong conclusion can be drawn from this comparison, because the color cue remained the same throughout the series,

TABLE 4. Choices of polymorphic fruits by Northwestern Crows. Entries in the table are the numbers of each morph chosen. R = red, G = gold, Y = yellow. Binomial tests were used for individual birds in Expts 21 and 23; statistical significance levels as in Table 3.

Bird	Rainier cherry (Expt 21) R:Y	Salmonberry (Expt 23) R:G	Bird	Salmonberry (Expt 39) R:G
2	3:3	1:1	1	16:0*
4	3:0	5:1 (*)	4	13:3*
5			5	8:8
6	4:2	1:5 (*)	6	15:1*
7	0:6*	0:6*	7	16:0*
8	4:2	1:3	8	13:3*
9	4:2			
10	1:5	4:1		
Total	19:20	12:17		81:15*
Het. χ^2	no test	no test		*

TABLE 5. Preferences of Northwestern Crows for dark and light domestic cherries. Binomial tests were used for the choices of individual birds, χ^2 tests for the totals; statistical significance levels as in Table 3.

A. Pairwise choices.		
Bird	Cherries (Expt 3) Dark : Light	Leaf cue (Expt 8) Dark : Light
2	4:0	5:4
3	—	5:4
4	8:0*	3:6
6	8:0*	6:3
7	7:1 (*)	3:6
8	7:1 (*)	6:3
9	8:0*	4:5
10	6:0*	2:7
Total	48:2*	34:38

B. Cross-cage experiment (Expt 16). Entries in the table are the ranks of the order in which fruits were taken (adding the ranks for four trials for each bird, and re-ranking those sums). If accessibility reduces the preference for dark cherries (by either option a or b, see text), the lowest scores should not appear in the columns labelled Dark.

Bird	Dark		Light	
	Up, side 1	Down, side 2	Up, side 2	Down, side 1
2	1	2	3	4
3	1	2	4	3
4	1.5	1.5	3	4
5	1	2	4	3
6	1	2	3.5	3.5
7	1	2	3.5	3.5
8	1	2	3.5	3.5
9	1	2	3.5	3.5
10	1	2	3	4
Mean	1.06	1.94	3.44	3.56

and the relative lack of shift of preference could reflect color choices rather than lipid choices.

In all of the foregoing experiments with lipid levels, the higher lipid level was indicated by a slightly less intense shade of red. Because the birds may have been exercising a hue preference rather than a lipid preference per se, we varied the experiment in two ways. (1) The experiments just described were followed by a cue-reversal experiment in which high lipid was indicated by a slightly darker shade of red (Expt 26). The birds were given two to eight trials to gain experience with the cue reversal and then retested. Birds #2 and 6 retained a significant preference for high lipid (and switched hues), and Birds #4 and #10 favored high lipid; Birds #7–9 showed no preferences during this relatively short series of trials. The birds' choices were significantly heterogeneous (Table 6). In 1991, seven birds were tested with reversed color cues (darker red high-lipid

fruits and lighter red low-lipid fruits; Expt 32; Table 6). Although the birds in aggregate evinced a preference for high lipid, heterogeneity was significant: Four birds favored high lipid, and three others showed no preference at all.

These results show that an inherent preference for lighter red cannot account for the earlier results from 1990, and that at least some birds seemed to be capable of learning an altered color signal to pick the preferred nutrient level. However, an alternative possibility is that the birds foraged by chance after the cue was altered, and that some picked one type of fruit and some, the other.

In both years we also examined lipid preferences in trials based on position rather than color cues (Expts 28, 33). In 1990, three birds favored high, one favored low, and three were indifferent. In 1991, three of six birds favored high lipid, one favored low, and two were indifferent. Birds in both years showed significant individual variation (Table 6). Thus, some birds appeared to learn to use position cues to locate favored food, but the frequency of apparent learners was no different from that expected by chance alone (i.e., six of 13 birds made the "right" choice; $\chi^2 < 2.0$, $P > 0.05$). It is not clear whether the observed variation among birds reflects variation in preference or in ability to learn position cues.

Trials using the mass method with a position cue (Expt 34) showed no indication of preference for high or low lipid and no differences among birds (ANOVA, lipid level by bird, means = high (51%): low (49%); bird $F_{5,36} = 0.64$, $P = 0.67$, lipid level $F_{1,36} = 0.02$, $P > 0.89$, interaction $F_{5,36} = 0.94$, $P = 0.47$).

Thus, there was a general tendency for birds to prefer high lipid levels, at least using color cues, but with individual variation (by the count method); no differences were seen by the mass method (position cue). Birds appeared to learn color cues more effectively than position cues.

Sugar experiments. The first two experiments in 1990 used corn syrup (a mixture of glucose and fructose) as sweetener, and slight hue differences as the indicator of nutrient level. In the first experiment (Expt 6), one bird preferred high sugar, one preferred low, and four had no significant preference; collectively, the birds had no preference and showed significant individual variation (Table 7). In the second experiment (Expt 7), five birds preferred high, and three had no preference; the collective results significantly

TABLE 6. Lipid-level preferences of captive Northwestern Crows. Count method only. Details of each experiment are given in Table 1. Expts 2–32 used hue-difference cues; Expts 28 and 33 used position cues. Chi-square tests were used, except where $n < 10$, when binomial tests were used. Statistical significance levels as in Table 3.

Bird	Expt 2 hi:lo	Expt 4 hi:lo	Expt 5 hi:lo	Expt 9 hi:lo	Expt 10 hi:lo	Expt 12 hi:lo	Expt 14 hi:lo
2	16:8(*)	10:4(*)	15:1*	11:5(*)	16:0*	11:4(*)	15:1*
3	11:12	11:5(*)	11:4(*)	13:2*	13:2*	10:6	7:9
4	18:6*	15:0*	16:0*	4:11(*)	13:3*	15:1*	5:11(*)
5	—	10:5	(4:4)	10:6	8:7	(6:1)(*)	4:8(*)
6	15:9	14:0*	15:0*	12:5(*)	12:2*	12:4*	11:4(*)
7	15:5*	15:0*	15:1*	16:1*	16:0*	16:0*	16:0*
8	11:8	7:9	8:8	14:4*	9:7	6:10	4:12*
9	20:4*	13:3*	14:0*	14:0*	8:6	12:4*	16:0*
10	22:1*	9:5	10:5	14:1*	9:8	13:2*	9:7
Total	128:53*	104:31*	108:23*	108:35*	104:35*	95:32*	87:52*
Het. χ^2	*	*	*	*	*	*	*

Bird	Expt 17 hi:lo	Expt 18 hi:lo	Expt 26 hi:lo	Expt 32 hi:lo	Expt 28 hi:lo	Expt 33 hi:lo
2 (1) ^a	16:0*	16:0*	16:0*	16:0*	14:2*	12:4*
3	10:9	—	—	12:4*	—	—
4	8:8	15:2*	16:0*	9:7	6:10	13:3*
5	—	—	—	7:9	—	15:1*
6	8:8	13:5(*)	14:2*	7:9	5:11(*)	8:8
7	12:4*	7:12	8:8	11:5(*)	16:0*	0:16*
8	11:4(*)	12:5(*)	10:6	14:2*	8:8	9:7
9	16:0*	16:0*	6:10	—	8:8	—
10	15:0*	12:2*	13:3*	—	15:0*	—
Total	96:33*	91:26*	83:29*	76:36*	72:39*	57:39*
Het. χ^2	*	*	*	*	*	*

Chi-square values for heterogeneity χ^2 tests; all $P < 0.05$: Experiments with hue-difference cues: Expt 2: 14.4, $df = 7$; Expt 4: 18.7, $df = 8$; Expt 5: 15.7, $df = 7$; Expt 9: 24.3, $df = 8$; Expt 10: 18.1, $df = 8$; Expt 12: 18.3, $df = 7$; Expt 14: 46.8, $df = 8$; Expt 17: 23.6, $df = 8$; Expt 18: 20.7, $df = 6$; Expt 26: 22.9, $df = 6$; Expt 32 (1991): 17.7, $df = 6$; Experiments with position cues: Expt 28 (1990): 33.4, $df = 6$; Expt 33 (1991): 35.4, $df = 5$.

^a Bird 2 in 1990, bird 1 in 1991 (Expts 32, 33).

TABLE 7. Sugar preferences of Northwestern Crows. Experiments 6, 7, 20, 24 (1990), and 35 (1991) used a hue-difference cue; Expt 36 (1991) used a position cue. Experimental details in Table 1. c.s. = corn syrup. Chi-square tests were used; statistical significance levels as in Table 3.

Bird	Expt 6 c.s. hi:lo	Expt 7 c.s. hi:lo	Expt 20 Sucrose hi:lo	Expt 24 Scurouse hi:lo	Expt 35 Glucose hi:lo	Expt 36 Glucose hi:lo	Expt 22 Lipid vs. c.s.	Expt 25 Lipid vs. sucrose
2 (1) ^a	4:7	10:3*	12:4*	15:1*	14:2* ^a	6:10 ^a	4:12*	8:8
3	—	10:4(*)	(4:4)	—	12:4*	5:11(*)	—	—
4	—	9:6	7:9	11:5(*)	8:8	12:4*	8:8	10:6
5	—	—	7:8	—	13:3*	9:7	—	—
6	13:1*	12:3*	8:8	11:4(*)	14:2*	15:1*	6:10	12:4*
7	4:12*	11:2*	8:8	2:14*	9:7	1:15*	6:10	12:4*
8	8:4	11:3*	8:8	11:4(*)	13:3*	1:15*	7:9	15:0*
9	8:7	6:8	9:7	15:1*	—	—	1:12*	0:15*
10	7:6	8:5	6:10	4:10(*)	—	—	8:8	12:4*
Total	44:37	77:34*	69:66	69:39*	83:29*	49:63	40:69*	69:41*
Het. χ^2	*	n.s.	n.s.	*	n.s.	*	n.s.	*

Chi-square values for heterogeneity χ^2 tests: Expt 6: 16.0, $df = 5$, $P < 0.01$; Expt 7: 7.5, $df = 7$, $P > 0.25$; Expt 20: 5.5, $df = 8$, $P > 0.50$; Expt 24: 36.5, $df = 6$, $P < 0.001$; Expt 35: 8.7, $df = 6$, $P > 0.10$; Expt 36: 42.5, $df = 6$, $P < 0.001$; Expt 22: 7.8, $df = 6$, $P > 0.25$; Expt 25: 35.9, $df = 6$, $P < 0.001$.

^a Bird 2 in 1990, bird 1 in 1991 (Expts 35, 36).

avored high sugar with little heterogeneity (Table 7).

In the first sucrose experiment (Expt 20), only one bird preferred high sugar, and collectively there was no preference with no significant heterogeneity. In the second (Expt 24), five birds preferred high and two preferred low. The collective results favored high sugar (Expt 24; $\chi^2 = 8.3$, $P < 0.01$) with significant heterogeneity (Table 7). With both corn syrup and sucrose, the second experiments produced more pronounced preferences, but the preferences were more consistent among birds for corn syrup than for sucrose. No bird consistently favored high sugar in both corn syrup and sucrose trials; one bird (#6) consistently favored high corn syrup and one (#2) consistently favored high sucrose, but most other birds made inconsistent choices.

In 1991, the sweetener used was glucose, with slight hue differences as a cue (Expt 35). Five birds favored high sugar, two were indifferent, and collectively there was a significant preference for high sugar, with little individual variation (Table 7). In the absence of hue differences, position was used as a cue (Expt 36). Individually, two birds favored high, three favored low, and two were indifferent. Individual variation was significant, and collectively the birds showed no preference.

Trials using the mass method with a position cue (Expt 37) showed that, in aggregate, the birds significantly favored high glucose levels with no significant variation among birds (67% vs. 33%; ANOVA, glucose level by bird, bird $F_{6,42} = 1.60$, $P = 0.17$, glucose level $F_{1,42} = 18.02^*$, $P < 0.01$, interaction $F_{6,42} = 1.87$, $P = 0.11$).

Thus, sugar preferences seemed to be even more variable than lipid preferences, and again color cues were somewhat more effective than position cues.

Sugars vs. lipids. In two experiments (Expts 22, 25), the crows were given a choice between artificial fruits with elevated levels of lipids or sugars (corn syrup or sucrose; Table 7). Heterogeneity among birds was significant in trials with sucrose but not with corn syrup. The five birds (#2, 4, 6, 7, 9) with the most consistent lipid preferences generally had variable preferences for high sugar levels, but did not necessarily favor lipid over sugar in Experiments 22 and 25 (Table 7). Two of seven birds favored corn syrup over lipid; the rest had no preference. Four of seven birds favored lipid over sucrose, one favored su-

crose over lipid, and two were indifferent. Thus, some birds preferred lipid over sucrose but not over corn syrup, although individual variation was evident. This suggests that any selection via feeding preferences for fatty fruits over sugary fruits is both variable and probably dependent upon the sugar composition.

Effect of accessibility on lipid and sugar preferences. When the oft-preferred high-lipid fruits were placed 13 cm below the less favored low-lipid fruits (Expt 11), all five tested crows favored the easy-to-reach low-lipid fruits (Table 8). When the distance between dishes was reduced to 6 cm (Expt 13), most birds still favored the easily accessible food or showed no preference; one bird (#2) now favored high lipid despite the need to reach a little farther (Table 8).

In the first cross-cage experiment (Expt 15), six of seven crows took food from the upper dishes, regardless of lipid level, flying across the cage to do so. One bird (#9) retained its preference for high lipid, although it had to fly across the cage and reach down to get the favored fruit. In the second cross-cage experiment with a higher lipid concentration (Expt 19), four of seven birds took food from the upper dishes. The other three birds all took high lipid from the upper dish first, but then crossed the cage and, with equal frequency, took the remaining high-lipid fruit from the lower position or the low-lipid fruit from the upper dish. Results of both experiments were similar, despite the difference in lipid concentration of the test fruits. Together, these cross-cage experiments show that the crows commonly forsook their high-lipid preference when it was made less accessible, although there was some variation in this tendency. The birds were unexpectedly willing to make cross-cage flights rather than making an extended reach downward.

Another accessibility experiment used food dishes in front and back of the test perch (Expt 27; Table 8). Four birds were offered high lipid in back, so they needed to reach behind or turn around to obtain the food. Three of four of these birds favored the easy-to-reach low-lipid fruit in front (two significantly so); Bird #2 had no significant preference, although it was the only bird willing to make a short reach (in Expt 13) to get the favored fruit. Two of the control birds favored the easily accessible high lipid, as expected, but one was indifferent.

When accessibility to high-sugar fruits was re-

TABLE 8. Effect of accessibility on the preferences of Northwestern Crows for lipid and sugar levels. For Expt 27, the birds were divided into two sets: the first set of four birds had high lipid fruits in back of the perch (less accessible), and the second set of three birds had high lipid fruits in front (easily accessible); in the experiment, the second set served as a control for the first set. Chi-square tests were used, except where $n < 10$, when binomial tests were used; statistical significance levels as in Table 3.

A. Pairwise tests.					
Bird	Expt 11 Long reach, lipid hi:lo	Expt 13 Short reach, lipid hi:lo	Expt 27 Front/back, lipid hi:lo	Expt 27 Control hi:lo	Expt 39 Short reach, glucose hi:lo
2 (1) ^a	1:7(*)	7:1(*)	5:10	—	14:2* ^a
3	0:8*	0:8*	—	—	—
4	0:8*	0:8*	1:15*	—	9:7
6	0:8*	2:6	—	16:0*	9:7
7	0:8*	4:4	2:14*	—	—
8	—	4:0	—	14:1*	11:5(*)
9	—	6:2	4:11(*)	—	—
10	—	2:6	—	8:8	—
Total	1:39*	25:35	12:50*	38:9*	43:21*
Het. χ^2	no test	no test	n.s.	*	n.s.
Compare to:	Expt 10	Expt 12	next column	previous column	Expt 35

Chi-square values for heterogeneity χ^2 tests: Expt 27 experimental: 2.76, $df = 3$, $P > 0.30$, control, 9.4, $df = 2$, $P < 0.01$; Expt 39: 4.19, $df = 3$, $P > 0.20$.

^a Bird 2 in 1990 (Expt 11–27), bird 1 in 1991 (Expt 39).

B. Cross-cage experiments; 5 × lipid difference in Expt 15, 8 × difference in Expt 19. Entries in table are ranks of the order in which fruits were taken (adding the ranks for 6 trials/bird in Expt 15, 4 trials/bird in Expt 19, and re-ranking those sums). If high lipid fruits are preferred regardless of accessibility, the lowest values should appear in the columns marked High. However, the lowest values occur in the columns marked Up in both experiments.

Bird	High		Low	
	Up, side 1	Down, side 2	Up, side 2	Down, side 1
Expt 15				
2	1	3.5	2	3.5
4	2	4	1	3
6	1	3	2	4
7	1	3	2	4
8	1.5	4	1.5	3
9	1	2	3	4
10	1	3	2	4
Mean	1.21	3.21	1.93	3.64
Expt 19				
2	1	2.5	2.5	4
4	1.5	3.5	1.5	3.5
6	1	3	2	4
7	2	3	1	4
8	1	4	2	3
9	1	2.5	2.5	4
10	1	2.5	2.5	4
Mean	1.21	3.00	2.00	3.79

duced (Expt 39), two birds retained a preference for high sugar, one bird lost its preference, and one retained a lack of preference (Table 8).

Thus, any preference for high levels of lipid usually disappeared when the favored fruits were made even slightly more difficult to reach, in marked contrast to the experiments with domestic cherries. The effect of accessibility on sug-

ar preferences was mixed; the considerable variability of sugar preferences makes this mixed result difficult to interpret.

Seed loads. Three crows showed no preference between artificial fruits with high and low seed loads (Expt 41; Table 9), but three others preferred those with high seed loads (Bird #1, 11:5 [*]; Bird #5, 13:3 *; Bird #6, 11:5 [*]). Collec-

TABLE 9. Food preferences of hand-raised crows.

A. Color preferences. Color symbols as in Table 3; N = natural color of foods. Entries in table are the numbers of artificial fruits consumed by each bird in each pairwise choice. Where possible, the intransitive portion of the array is shown, in parentheses when contiguous portions are involved, and with five entries when the ends of the array are involved. Statistical significance levels as in Table 3.

Bird	Train- ing food	R:G	R:Y	R:B	B:G	B:Y	G:Y	Transitivity
1	R	14:2*	15:1*	16:0*	10:6	11:7	4:12*	intransitive; R > (B, G, Y)
2	R	8:10	14:3*	10:9	13:4*	15:2*	14:3*	intransitive; R = (B ≥ G) > Y
3	Y	12:4*	15:2*	9:9	8:10	13:4*	16:0*	intransitive; (R, B, G) > Y
4	Y	12:6	14:2*	11:7	5:10	16:0*	12:4*	R = B = G > Y
5	Y	13:3*	16:0*	11:6	11:5(*)	10:0*	12:4*	R = B > G > Y
6	N	13:4*	11:6	7:10	11:5(*)	15:2*	14:2*	intransitive; R = B > G > Y = R
7	N	16:0*	16:0*	16:0*	13:4*	6:12	0:16*	R > B = Y > G
8	N	12:6	16:0*	8:8	11:6	16:0*	16:0*	R = B = G > Y
Total		100:35*	117:14*	88:49*	82:50*	102:27*	88:41*	
Het. χ^2		(*)	n.s.	*	n.s.	*	*	

Chi-square values for heterogeneity χ^2 tests, all df = 7: R/G 12.93, 0.05 < P < 0.10; R/Y 6.8, n.s.; R/B 28.84, P < 0.001; B/G 10.62, n.s.; B/Y 25.93, P < 0.001; G/Y 62.26, P < 0.001.

B. Lipid and sugar preferences.

Bird	Lipids			Corn syrup	
	Set 1 hi:lo	Set 2 hi:lo	Set 3 hi:lo	Set 1 hi:lo	Set 2 hi:lo
1	26:17	33:8*	34:6*	3:13*	0:16*
2	30:11*	29:13*	30:10*	2:14*	5:11(*)
3	25:17	24:19	30:10*	5:11(*)	1:15*
4	26:16(*)	26:15(*)	29:11*	5:11(*)	5:11(*)
5	26:16	21:21	14:26(*)	3:13*	7:9
6	13:3*	13:28*	11:29*	11:5(*)	12:4*
7	12:33*	20:21	26:14(*)	4:12*	7:9
8	4:37*	4:36*	2:38*	11:5(*)	11:5(*)
Total	162:176	170:161	176:144*	44:84*	48:80*
Het. χ^2	*	*	*	*	*

Chi-square values for heterogeneity χ^2 tests, all df = 7, all P < 0.005: Lipids, Set 1: 60.03, Set 2: 52.74, Set 3: 92.2; Corn syrup, Set 1: 22.00, Set 2: 31.50.

tively, the birds preferred high seed loads ($\chi^2 = 5.0$, P < 0.05); the heterogeneity test was not significant.

Do crows use leaves as cues to fruit selection? Preceding trials (Expt 3) showed that dark-red, sweet were strongly preferred to light-red, tart domestic cherries. We then gave the birds two training trials with dark cherries placed on top of alder leaves and light cherries placed on cottonwood leaves to allow the birds the possibility of associating the favored cherries with a particular type of leaf. The preference for dark cherries was maintained (overall $\chi^2 = 14.2$, P < 0.05). The next series of trials placed the cherries beneath their respective associated leaf types, and the birds had to remove the leaf or reach under it to see and obtain the cherry. Each bird had at

least seven trials in which to learn the association, and no bird evinced a preference in either direction during the learning phase. If the birds had learned to use leaves as a searching cue during the training trials, they should exhibit a preference for leaves covering the dark cherries in the experimental trials. However, in the last nine (experimental) trials (Expt 8), neither individually nor collectively did the birds show a significant preference (Table 5).

Experiments with hand-raised crows. The hand-raised juvenile crows all favored red or blue fruits, regardless of the color with which they were experienced; several ranked green equally with red and blue (Table 9). Five (#2, 3, 4, 5, 8) avoided yellow and one avoided green. Four of the eight made transitive choices. Thus, food colors to

which the birds were exposed from the time their eyes opened until the time of testing had no detectable effect on food-color choices when they were able to feed themselves.

The hand-raised juveniles showed a slight but variable tendency to favor high-lipid fruits (with color cues). In a long series of 30 trials using the count method, two birds (jv #2, 4) favored high-lipid fruits throughout, three birds (jv #1, 3, especially 7) increasingly favored high; one (jv #8) consistently favored low lipid, and two (jv #5, 6) shifted toward low (Table 9). Trials using the mass method showed no collective tendency to favor high lipid, although individual preferences differed (ANOVA, lipid level by bird; 54% vs. 46%, bird $F_{7,48} = 3.07^*$, $P < 0.01$, lipid level $F_{1,7} = 0.01$, $P > 0.75$, interaction $F_{7,48} = 6.72^*$, $P < 0.001$).

Juveniles showed some collective tendency to favor low sugar (corn syrup; count method; Table 9), although heterogeneity was significant. There was relatively little change between the first four and the last four trials in a series of ten. By the mass method, there was no collective preference for sugar levels and little variation among individuals (ANOVA, sugar level by bird, 43% vs. 57%, bird $F_{7,48} = 1.01$, $P = 0.44$, glucose level $F_{1,7} = 1.24$, $P > 0.18$, interaction $F_{7,48} = 3.88^*$, $P < 0.002$).

Experiments with free-ranging crows. (1) A cafeteria experiment with natural fruits was conducted with one wild flock in 1991. In a series of six trials, the crows favored early blueberry in two trials, early blueberry and red salmonberry in one trial, and red salmonberry, gold salmonberry, and twisted-stalk in one trial each. These results show some similarity to the aviary experiments, in that the same set of fruits was top-ranked, if all experiments are considered. However, early blueberry was seldom favored by aviary birds in 1991, although the wild flock in the same year often chose this species.

(2) Color preferences. In 1990, a single experiment with one flock in downtown Juneau showed that more red and yellow than green and blue artificial fruits were eaten. In 1991, we tested several flocks of crows located at four points on the Juneau shoreline (Table 10). All four flocks included red as a first-choice hue. Yellow was favored at least as much as red for one flock, but lower-ranked for the others. Blue was low-ranked for three of four flocks, and relatively little was eaten by the fourth flock, in contrast to most

TABLE 10. Color preferences (mass method) of free-ranging Northwestern Crows. Data are mean percents of total amount eaten for each color of artificial fruits in four trials. ANOVA: Model $F_{18,45} = 4.51^*$, $P = 0.0000$, flock $F_{3,45} = 0.02$, $P = 0.99^+$, color $F_{3,45} = 21.06^*$, $P = 0.0000$, interaction $F_{9,45} = 1.99$, $P = 0.063^*$.

Flock	Red	Blue	Green	Yellow
Eagle Beach	86	10	2	2
Lena Beach	63	0	25	12
Sheep Creek	44	0	0	56
Sandy Beach	74	1	5	20

aviary birds (including juveniles). Green was low-ranked by three of four flocks, although one flock ranked it second. The average ranks were R (1.3) > Y (2.4) > G (3.0) > B (3.4). The tendency to prefer red is similar to that of the 1990 aviary experiments, but not those of 1991. Aviary crows often rejected yellow, like three of the wild flocks. Thus, the color-rankings of single, captive crows did not necessarily resemble those of free-ranging groups of foraging crows.

(3) Polymorphic natural fruits. Three flocks (four trials each) were tested on the color morphs of salmonberry in 1991. All three flocks preferred red to gold (Lena Point 42:12*; Sheep Creek 35:20*; Sandy Beach 45:12*; all $\chi^2 > 4.0$, $P < 0.05$; no significant heterogeneity), as did most captive crows in 1991 (but not 1990).

(4) Lipid and sugar choices. One flock in 1990 and four in 1991 showed no collective tendency to favor high-lipid food and no variation among flocks (ANOVA, lipid level by flock in 1991, means = high (49%) : low (51%); flock $F_{3,24} = 1.13$, $P = 0.36$, lipid level $F_{1,24} = 0.13$, $P > 0.72$, interaction $F_{3,24} = 1.04$, $P = 0.39$). Four flocks in 1991 exhibited no significant general preferences for glucose content and little variation among flocks (ANOVA, glucose level by flock, means = high (49%) : low (51%); flock $F_{3,24} = 2.68$, $P = 0.07$, glucose level $F_{1,24} = 0.002$, $P > 0.97$, interaction $F_{3,24} = 0.92$, $P = 0.44$). Thus, group-foraging, untrained wild birds appeared to show less overall preference for high-nutrient levels than captive crows.

(5) Seed load. Four flocks in 1991 were offered artificial fruits with and without enclosed seeds, with a slight color cue (four trials for each flock). There was no significant general tendency to favor fruits with low seed loads, but flocks varied (Eagle Beach 73 with seeds : 27 without seeds; Lena Point 59:41; Sheep Creek 54:46; Sandy

Beach 54:46; mean 60:40; ANOVA: flock $F_{3,24} = 7.29^*$, $P = 0.001$, seed load $F_{1,3} = 0.45$, $P > 0.50$, interaction $F_{3,24} = 9.18^*$, $P = 0.000$). Thus, neither free-ranging nor captive crows avoided the fruits with the indigestible ballast.

DISCUSSION

Selectivity for fruit traits. Captive crows were often selective of the fruits (both natural and artificial) that they ate. The favorite natural fruits varied among individuals and were not distinguished by any obvious characteristics, such as size, seed load, or lipid content, although they were commonly either red or blue. Choices among natural fruits in the cafeteria experiment did not necessarily reflect color preferences as exhibited in earlier experiments.

Color preferences of captive crows were also variable and often intransitive. The relationship of color preferences to the colors of native fruits is not close. Most species of native fruits in southeastern Alaska have red fruits, but blue fruits (i.e., of *Vaccinium* spp.) are often very abundant. Several birds favored red or blue fruits, but some also preferred green, although no mature fruits native to the region are that color. Although yellow fruits occur in the region, they were often rejected (almost as often as green) by individual crows. Extensive individual variation and generally poor correspondence with expectations also characterized the choices of other frugivores (Willson et al. 1990, Levey and Karasov 1989, Jung 1992, Willson, unpubl. manuscript). These results suggest that the evolution of fruit colors may be driven chiefly by factors other than color preferences. The most likely factor related to avian foraging is the possibly greater conspicuousness/detectability of certain colors (Willson and Whelan 1990). In some instances, however, familiarity with certain colors or color patterns may foster feeding preferences (Raymond and Allen 1990) and might contribute to the partial tendency to favor the more common red morph of salmonberry; however, this would require that the birds remembered the fruits from the summer before they were captured. Experiments with hand-raised crows also demonstrated that nestling experience with particular food colors does not appear to lead to food color preference (or aversions) when the birds mature.

Many of the experiments used color cues to indicate fruit type. Color cues might also indicate state of fruit maturity in the wild; for most fruits,

riper fruits are darker than immature fruits. If captive birds interpret darker hues as a sign of maturity and prefer mature fruits, they should generally prefer whatever fruit type is darker. As we have shown, however, this was not a general tendency. Furthermore, the captive crows were sometimes able to switch cues to maintain a preference for particular fruit types, suggesting that the use of a fruit-maturity signal, if present, was flexible. This result contrasts with that for *Turdus migratorius*, which appeared to use darker hues more successfully than lighter ones (Willson, unpubl. manuscript).

The hypothesis that fruit-foraging birds may favor lipid-rich fruits (Stiles 1980) received some support from experiments with both adult and juvenile captive crows. However, again we observed considerable individual variation. Furthermore, the tendency to prefer high-lipid fruits was dependent on the kind of foraging cue available: the trend was stronger with a color cue than with a position cue (see also Schuler 1983). In addition, most birds completely lost this preference if the favored fruits were made even slightly less accessible or when high-sugar fruits (especially those with corn syrup) were available. Crows are capable of very strong preferences, however, as shown by the experiments with domestic cherries. These results suggest that, even though lipid preferences may occur, they are quite weak. They also may be difficult to exercise in natural situations, where position cues (such as location on a plant) are common, color cues are not obviously associated with lipid content, many fruits have high sugar levels, and accessibility varies enormously.

Adult crows often preferred high-sugar fruits (with color but not position cues), but with much variation within and among birds. Reduced accessibility had mixed effects on preference; in contrast to the lipid experiments, some individuals retained a preference for high sugar even when accessibility was reduced. Although species differ in their responses to sugar type and concentrations, several kinds of passerine birds are known to prefer hexose sugars, especially glucose, to the disaccharide sucrose, probably because of post-ingestion cues resulting from a greater ability to utilize glucose (Schuler 1983, Martínez del Río et al. 1988, Martínez del Río and Stevens 1989, Martínez del Río et al. 1989, Martínez del Río 1990b, Levey and Grajal 1991, Brugger and Nelms 1991). We did not explicitly examine the preferences of crows for hexose vs.

disaccharide, but we detected little aversion of adults to either sugar, which may indicate that crows are able to utilize both kinds of sugars. In contrast to the adults, juvenile crows did not tend to favor high-sugar fruits, possibly indicating developmental changes in preferences and/or requirements or a longer learning period for sugars than for lipids. Some individual variation in digestive capacity should be expected (e.g., Shuman et al. 1989), and may contribute to the observed variation among birds.

The experimental crows showed no tendency to avoid fruits with high seed loads. The large body size of the birds may reduce the cost of dealing with ballast (see Levey and Grajal 1991), or the experimental conditions may not have encouraged fine-tuned choices with respect to this trait. However, similar experiments with captive *Turdus migratorius* also showed no preference for low seed loads (Willson, unpubl. manuscript).

The crows showed no tendency to use simple foliar cues in making fruit choices (as shown by R. Jung, pers. comm., for other species). The failure to learn foliar cues in our cherry experiment, where preferences were quite strong, appears to contrast with the rapid learning of cues described for carrion crows (*C. corone*; Croze 1970). The use of foliar cues for fruit-foraging would be particularly interesting, perhaps, in eastern North America, where the fruits of sympatric *Menispermum* and *Vitis* look very similar to human eyes, but the leaves are very different.

Free-ranging crows exhibited color preferences only partially similar to those of captive crows (red ranked highest overall for both captive and wild crows in 1991, but ranks of other colors differed). Preferences for native fruits also showed some similarities in aviary and wild birds. Seed-load preferences in captive and wild birds were virtually identical, although the difference was significant for captives and not for wild crows (captive: 61% > 39%; wild 60% vs. 40%). Lipid and glucose preferences were not expressed in the wild-crow experiments (49% vs. 51%), but captive crows collectively preferred high lipid-fruits in all experiments in Table 6 and high glucose in Expt 35 (Table 7). Formal statistical comparisons of these collective lipid and sugar choices by captive and wild crows are infeasible, because of the differences in methods. Nevertheless, for both lipid and glucose experiments, the pattern is that captive crows, particularly some individuals, showed some discrimination, but wild ones did not.

That flocking crows in the wild appeared to show less selectivity than aviary crows (see also Rowley et al. 1989) might be explained by dominance interactions within the foraging group. However, this interpretation in its simplest form is complicated by the fact that the apparently reduced selectivity was observed for lipid and sugar content, but not for color or fruit morph. Even group-foraging crows in the wild exhibited some color preferences, as did captive flocks of Cedar Waxwings (*Bombycilla cedrorum*; McPherson 1988), suggesting that group foraging per se is insufficient to eliminate selectivity. Differences in lipid and sugar content were not discernible externally, except by association with a slight color cue. Wild crows lacked the experience required to learn to associate the cue with the nutrient content. The lack of experience was probably more important than group foraging in explaining the apparent indifference of wild crows to nutrient content. In any case, the ability of individual crows to exercise a preference is clear from the aviary experiments; to the extent that group foraging or learning lags eliminate such preferences, selection in natural conditions is weakened. Furthermore, if wild crows generally require a visual cue to identify fruits with higher nutrient levels, the natural variation of fruit appearance within a crop or within a species does not appear to offer such cues. At least to human eyes, conspecific fruits offer little external indication of nutrient concentrations of the pulp and, thus, little basis for a visually determined choice on the basis of appearance (apart from fruit size). Under these conditions, natural selection for fruit nutrients must be impeded. However, if birds learn via digestive feedback (e.g., Levey and Karasov 1989) to associate nutritional levels with fruit location, some selection for nutrient content could occur, provided that fruits remain available long enough for this feedback and learning to occur and that the birds return to forage from the same plants.

Taken together, these experiments show that Northwestern Crows exhibit some selectivity for fruits. However, individual variation in choice behavior is great in many situations, and many choices related to nutrient content of the fruits can be altered readily. Furthermore, wild crows only sometimes exhibit the same choices as captive birds (see also McPherson 1988, Levey et al. 1984). Thus, any selection by avian frugivores (here represented by Northwestern Crows) for particular fruit traits appears to be weak and

variable. Weak or inconsistent preferences (and avoidances) do not completely vitiate a claim for current selection, however, because the "proper" conditions for strong choices may not have been provided by the experimenter. Nevertheless, if weak or inconsistent choices are recorded for a variety of frugivores in diverse conditions, the case against present-day selection pressures is bolstered. Other studies of fruit selectivity also suggest weak or variable selection by various sets of frugivores in a variety of circumstances (Willson et al. 1990; Willson and Whelan 1993; Herrera 1986, 1988; Jordano 1987, 1989; Jung 1992). Although physiological constraints may provide some selection on fruit traits such as sugar composition or seed-packaging (Levey and Grajal 1991, Martínez del Río 1990b, Martínez del Río et al. 1988), too few birds have yet been examined to establish this possibility (Martínez del Río and Stevens 1989).

Methodological considerations. Aviary experiments with captive birds are often the only way to test single birds with small numbers of variables, but the results may or may not resemble those from the more complex natural world. Dissimilar results need not invalidate the results from captives, but indicate at least that the ubiquitous "other factors" are probably at work. In some cases, results from captives can indicate what the animals can do, whereas the results from free-ranging animals may indicate what they actually do. For Northwestern Crows, we have shown that results from captive birds often provide no indication of what the wild birds do.

For any set of experiments of this type, we must bear in mind that the results may be conditional upon the specific conditions of the experiment. Thus, our conclusions concerning lipid preferences actually deal only with corn oil; different results could be obtained if some other vegetable oil were used (only vegetable oils are relevant to studies of fruit selectivity). Likewise, we used certain colors of certain intensities, and the color preferences exhibited could be specific to those particular shades. However, our experience suggests that the crows' choice behavior did not depend on subtly different shades of red, or of blue (see also Brugger and Nelms 1991).

The count method and the mass method sometimes yielded different results. It is tempting to try to relate this to the distribution of fruits in nature, where some fruits are highly aggregated and other are very dispersed in space. However,

we do not know whether the different outcomes, in fact, reflect the difference in method or perhaps reflect the kind of variation we often observed between trials conducted on different days (see the series of lipid experiments, for example, in Table 7). Many of the captive birds exhibited variation in responses at different times, for reasons unknown. Although it is possible that some of this variation results from subtle differences in fruit quality or from differences in physiological condition or changing requirements of the birds, we have the opinion, totally subjective, that intelligent birds such as crows may sometimes elect to vary their responses for their own subjective reasons (just as animals in zoos are known to do). Whatever the reason, seemingly erratic behavior indicates a need for caution in interpreting the experimental results.

ACKNOWLEDGMENTS

We are grateful to Stacy Porvasnik for her particularly good assistance with the aviary experiments, to K. C. Halupka and K. E. Sieving for helpful consultation, and to C. J. Whelan and D. J. Levey for constructive comments on the manuscript.

LITERATURE CITED

- ARMSTRONG, R. H. 1990. Guide to the birds of Alaska. 3rd ed. Alaska Northwest Books, Anchorage, AK.
- BARROWS, W. B. 1889. The food of crows. USDA Annual Report 1888:498-535.
- BENT, A. C. 1964. Life histories of North American jays, crows, and titmice. Dover, New York.
- BRUGGER, K. E., AND C. O. NELMS. 1991. Sucrose avoidance by American Robins (*Turdus migratorius*): implications for control of bird damage in fruit crops. Crop Prot. 10:455-460.
- CROZE, H. 1970. Searching image in Carrion Crows. Zeitschr. f. Tierpsych. 5:1-85.
- DENSLOW, J. S., AND T. C. MOERMOND. 1982. The effect of accessibility on rates of fruit removal from tropical shrubs: an experimental study. Oecologia 54:170-176.
- DENSLOW, J. S., D. J. LEVEY, T. C. MOERMOND, AND B. C. WENTWORTH. 1987. A synthetic diet for fruit-eating birds. Wilson Bull. 99:131-135.
- HERRERA, C. M. 1986. Vertebrate-dispersed plants: why they don't behave as they should, p. 5-18. In A. Estrada and T. H. Fleming [eds.], Frugivores and seed dispersal. Junk, Dordrecht, The Netherlands.
- HERRERA, C. M. 1988. The fruiting ecology of *Osyris quadripartita*: individual variation and evolutionary potential. Ecology 69:233-249.
- HERRERA, C. M. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. Am. Nat. 140:421-446.

- JORDANO, P. 1987. Avian fruit removal: effects of fruit variation, crop size, and insect damage. *Ecology* 68:1711-1723.
- JORDANO, P. 1989. Pre-dispersal biology of *Pistacia lentiscus* (Anacardiaceae): cumulative effects of seed removal by birds. *Oikos* 55:375-386.
- JUNG, R. E. 1992. Individual variation in fruit choice by American Robins (*Turdus migratorius*). *Auk* 109:98-111.
- KALMBACH, E. R. 1918. The crow and its relation to man. USDA Bull. 621.
- KALMBACH, E. R. 1920. The crow in its relation to agriculture. USDA Farmer's Bull. 1102.
- LEVEY, D. J., T. C. MOERMOND, AND J. S. DENSLow. 1984. Fruit choice in neotropical birds: the effect of distance between fruits on preference patterns. *Ecology* 65:844-850.
- LEVEY, D. J., AND A. GRAJAL. 1991. Evolutionary implications of fruit-processing limitations in Cedar Waxwings. *Am. Nat.* 138:171-189.
- LEVEY, D. J., AND W. H. KARASOV. 1989. Digestive responses of temperate birds switched to fruit or insect diets. *Auk* 106:675-686.
- MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. American wildlife and plants. Dover, New York.
- MARTÍNEZ DEL RIO, C. 1990a. Sugar preferences in hummingbirds: the influence of subtle chemical differences on food choice. *Condor* 92:1022-1030.
- MARTÍNEZ DEL RIO, C. 1990b. Dietary, phylogenetic, and ecological correlates of intestinal sucrase and maltase activity in birds. *Physiol. Zool.* 63:987-1011.
- MARTÍNEZ DEL RIO, C., B. R. STEVENS, D. E. DANEKE, AND P. T. ANDREADIS. 1988. Physiological correlates of preference and aversion for sugars in three species of birds. *Physiol. Zool.* 61:222-229.
- MARTÍNEZ DEL RIO, C., W. H. KARASOV, AND D. J. LEVEY. 1989. Physiological basis and ecological consequences of sugar preferences in Cedar Waxwings. *Auk* 106:64-71.
- MARTÍNEZ DEL RIO, C., AND B. R. STEVENS. 1989. Physiological constraint on feeding behavior: intestinal membrane disaccharidases of the starling. *Science* 243:794-796.
- MCPHERSON, J. M. 1988. Preferences of Cedar Waxwings in the laboratory for fruit species, colour and size: a comparison with field observations. *Anim. Behav.* 36:961-969.
- MOERMOND, T. C., AND J. S. DENSLow. 1983. Fruit choice in neotropical birds: effects of fruit types and accessibility on selectivity. *J. Anim. Ecol.* 52:407-420.
- PETERSON, C. H., AND P. E. RENAUD. 1989. Analysis of feeding preference experiments. *Oecologia* 80:82-86.
- RAYMOND, D. L., AND J. A. ALLEN. 1990. Wild birds prefer the familiar colour pattern when feeding on similar artificial morphs. *Oikos* 57:175-179.
- ROWLEY, I., E. RUSSELL, AND M. PALMER. 1989. The food preferences of cockatoos: an aviary experiment. *Aust. Wildl. Res.* 16:19-32.
- SAKAI, H. F., AND J. R. CARPENTER. 1990. The variety and nutritional value of foods consumed by Hawaiian Crow nestlings, an endangered species. *Condor* 92:220-228.
- SAKAI, H. F., C. J. RALPH, AND C. D. JENKINS. 1986. Foraging ecology of the Hawaiian Crow, an endangered generalist. *Condor* 88:211-219.
- SCHULER, W. 1983. Responses to sugars and their behavioural mechanisms in the starling (*Sturnus vulgaris*). *Behav. Ecol. Sociobiol.* 13:243-251.
- SHUMAN, T. W., R. J. ROBEL, J. L. ZIMMERMAN, AND K. E. KEMP. 1989. Variance in digestive efficiencies of four sympatric avian granivores. *Auk* 106:325-326.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2nd ed. Freeman, San Francisco.
- STILES, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *Am. Nat.* 116:670-688.
- WILLSON, M. F., AND C. J. WHELAN. 1990. The evolution of fruit color in fleshy-fruited plants. *Amer. Nat.* 136:790-809.
- WILLSON, M. F., AND C. J. WHELAN. 1993. Variation in dispersal phenology of a bird-dispersed shrub, *Cornus drummondii*. *Ecol. Monogr.* 63:151-172.
- WILLSON, M. F., D. A. GRAFF, AND C. J. WHELAN. 1990. Variation in food-color preference of some frugivorous birds. *Condor* 92:545-555.