DIET SELECTION BY YEARLING NORTHWESTERN CROWS (*CORVUS CAURINUS*) FEEDING ON LITTLENECK CLAMS (*VENERUPIS JAPONICA*)

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ABSTRACT.—Yearling and adult Northwestern Crows (*Corvus caurinus*) used similar methods in searching for buried Japanese littleneck clams (*Venerupis japonica*) and therefore encountered similar proportions of different-size clams. The mean size of clams eaten by yearling birds was significantly smaller than the mean of those eaten by adults despite the similar proportions encountered. The estimated lower limit of the diet (the smallest clams eaten by the average bird) was 25.5 mm for yearlings and 29.0 mm for adults. Yearlings took more time to find and handle clams and required more drops to break them open than did adults. Consequently, yearlings achieved only one-third the rate of net energy intake of adults feeding from the same food source. However, the extended diet consumed by the yearlings yielded close to the maximum possible rate of energy intake, within the limits imposed by their inefficiency. *Received 18 April 1986, accepted 4 November 1986.*

A NUMBER of avian species drop hard-shelled prey to gain access to the edible parts (Oldham 1930, Priestley 1947, North 1948, Tinbergen 1953, Barash et al. 1975, Kent 1981, Maron 1982). A predator using this technique must make a number of decisions if it is to realize the maximum rate of net energy intake for its effort. It must choose the best substrate on which to drop the prey (Barash et al. 1975, Siegfried 1977, Zach 1979), the height from which to drop it (Siegfried 1977, Zach 1979, Maron 1982), how many times to drop it before giving up if it does not break (Zach 1979), and which sizes of prey to drop (Zach 1979, Kent 1981, Richardson and Verbeek 1986).

Immature individuals of a number of species perform such complex tasks less efficiently than do adults (Orians 1969, Recher and Recher 1969, Dunn 1972, Buckley and Buckley 1974, Barash et al. 1975, Siegfried 1977, Verbeek 1977, Ingolfson and Estrella 1978) and therefore achieve a lower rate of net energy intake. It is predicted from the classical, sequential encounter model of diet selection (MacArthur and Pianka 1966, Krebs and McCleery 1984) that such inefficiency should result in the predator incorporating a wider range of prey items into its diet. Adult Northwestern Crows (*Corvus caurinus*), feeding on Japanese littleneck clams (*Venerupis japonia*), obtain close to the theoretical maximum yield by including all clams longer than 29.0 mm in their diet (Richardson and Verbeek 1986). We compared the efficiency of adult and yearling crows in searching for and handling littleneck clams, we determined the size range of clams eaten (diet breadth) of yearling crows, and then we compared the rate of energy intake from this diet with the rate they could expect to gain by taking any other size range of littleneck clams.

METHODS

The data were collected on Mitlenatch Island, British Columbia, from late April to early August of 1978–1982. Butler (1974) and Brooke et al. (1983) described the island in more detail. About 60 nesting pairs, 20 yearlings, and a small, unknown number of nonnesting adult Northwestern Crows live on the island from early spring to late summer (Butler et al. 1984). A yearling was defined as a bird in its first spring and summer after fledging. Yearlings are similar morphologically to adults but can be distinguished by a brown cast to their plumage, particularly on the wing tips and tail coverts (Verbeek and Butler 1981). The extent to which this population of crows exploits the clam bed varies, but for many of the birds it is a major foraging area (Butler 1974, 1980). The clam bed, located in one of two small bays on the island, is bounded on two sides by flat rock outcrops and on its upper edge by a pebble beach. The crows usually fly to these rocks or the beach to break open clams. No other prey types are taken from the clam beds. A small proportion of the clams that have been dug up are carried to some other part of the island and stored. Stored clams are longer, on average, than those consumed at the clam bed (James and Verbeek 1984), but this should not have affected our analysis, which was concerned only with the choice of clams to be eaten at the clam bed.

Clams available.—Clam length, taken as the greatest overall shell dimension, was measured to the nearest 0.1 mm with vernier calipers. All measurements are given ±1 SE unless stated otherwise.

The length-frequency distribution of live clams was determined from 202 sample quadrats, each 25 × 25 × 15 cm deep, located at regular intervals across the clam bed. No systematic error was introduced by this regular sampling method as there were no consistent differences in the spatial distributions of large and small clams (Richardson 1983). The rate at which clams were encountered by foraging crows depended on the length and burial depth of the clams as well as the searching methods employed by the birds. The techniques used in quantifying these search methods and calculating differences in the availability of clams to yearling and adult crows were detailed by Richardson (1985).

Clams eaten.—The length-frequency distribution of clams eaten by the two age classes was established by collecting the empty shells directly after the crows had finished feeding from them. We also collected intact clams that the crows dug out of the beach but then rejected. The proportion of each length class eaten could not be measured directly, because the numbers present in the diet and in the total prey population were estimated by different methods. Length-specific mortality rates were therefore estimated from forage ratios (Ivlev 1961), defined as the ratio of the proportion a particular prey type constitutes of the predators' diet to the proportion it constitutes of the total prey population. The largest clams were consumed whenever encountered by either yearlings or adults, and diet breadth can be conveniently expressed as the smallest size class of clams included in the diet. A single forage ratio was calculated for all length classes that were eaten whenever encountered. The mortality of other length classes was then estimated by expressing the forage ratio of each length class as a percentage of the forage ratio for the length classes that were eaten whenever encountered. The LD 50 from probit analysis (Finney 1971) of these mortalities was taken to represent the length of clams taken 50% of the time they were encountered by an average crow.

Search and handling times.—The foraging process was divided into six parts on the basis of energetic costs (Richardson and Verbeek 1986). These parts (search, first drop flight, examination between flights, additional drop flights, meat extraction, and return to the clam bed) were timed to the nearest 0.1 s with a stop watch. The number of drops needed to open a clam and the time required to extract meat from the broken shell were measured by direct observation. The relationship between each of these activities and clam length was determined by collecting and measuring the shell immediately after the observations had been made. The duration of other parts of the foraging process were assumed to be independent of clam length.

Energetic costs.—A value of 20,000 J/g dry mass was used for the energetic content of the soft tissues of a clam (Cummins and Wuycheck 1971, James and Verbeek 1984), and the crows were assumed to have a digestive efficiency of 75% (Ricklefs 1974). Irving et al. (1955) determined the basal metabolic rate of the Northwestern Crow as 3.6 J/s, and Zach (1978) used multipliers of 9 × BMR for flying, 4 × BMR for digging, and 2 × BMR for other foraging activities (see also Zach 1978). The mass of the longest littleneck clams was only about 4% of the total mass of an adult crow, so a bird's energetic cost of flying while carrying a clam was assumed to be independent of the length of the clam.

The optimal, energy-maximizing diet.—The rate of net energy intake for adults and yearlings was calculated from the sequential, random encounter model of diet selection (Krebs and McCleery 1984, Richardson and Verbeek 1986). The rate of net energy intake for both adults and yearlings feeding on all other possible diet breadths was then calculated using this model. The diet breadth that provided the maximum rate of net energy intake for each age group was then compared with the observed limit (LD 50 ± SE from probit analysis) for that age class.

RESULTS

Clams available.—Crows searched for clams with their bills, either by thrusting vertically into the beach (probing) or by making lateral (digging) motions. The proportions of probes made by yearlings (60% of 569 searches) and adults (55% of 642 searches) were similar ($\chi^2 = 2.62$, df = 1, $P > 0.1$). There was no difference in the depth-frequency distributions of either digs (Fig. 1a) or probes (Fig. 1b) made by the two age classes ($\chi^2 = 7.06$, df = 3, $0.1 > P > 0.05$, and $\chi^2 = 7.4$, df = 3, $0.1 > P > 0.05$, respectively). Yearlings and adults were considered therefore to encounter similar length-frequency distributions of these clams (Fig. 2a), and their diets could be compared directly.

Clams eaten.—The size range of 174 clams eaten by yearlings was 22.0–39.0 mm, very similar to the range of 24.0–42.0 mm for 575 clams eaten by adults and collected concurrently (Fig. 2b). The median length of clams eaten by yearlings (31.3 mm), however, was significantly smaller (Mann-Whitney *U*-test, $P < 0.001$) than the median length of those eaten by adults (33.0 mm), effectively decreasing the lower limit of the yearlings diet to 25.5 ± 0.35 mm compared

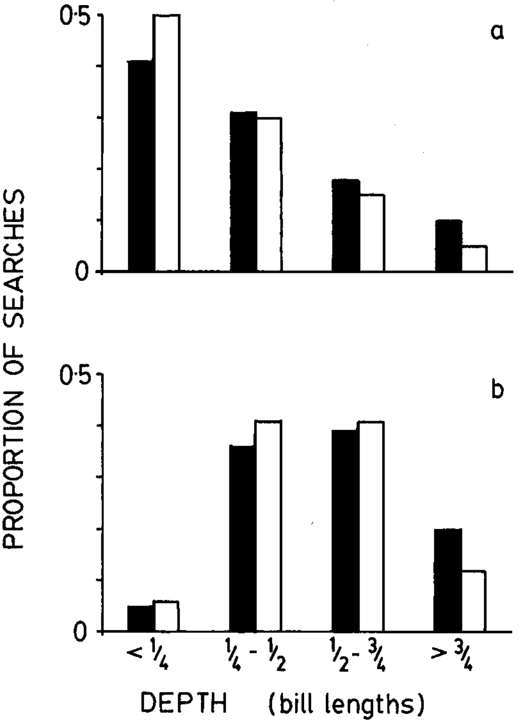

Fig. 1. Comparison of the depth-frequency distribution of (a) 289 digs by adult and 230 by yearling Northwestern Crows searching for littleneck clams and (b) 353 probes by adult and 339 by yearling crows. Solid bars = adults, open bars = yearlings.

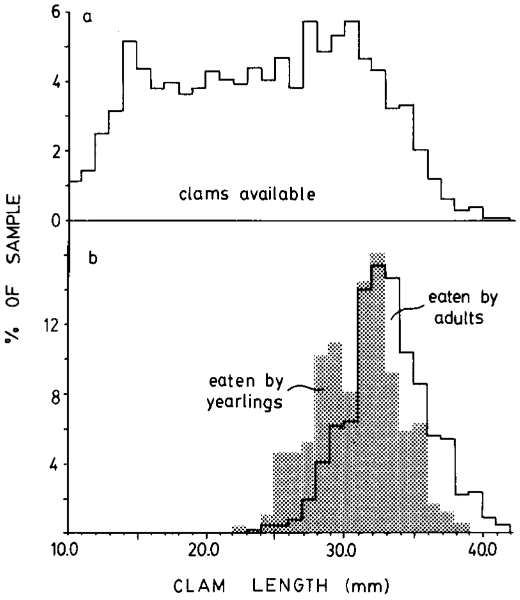

Fig. 2. Length-frequency distribution of littleneck clams available to adult and yearling Northwestern Crows feeding in Well Bay, Mitlenatch Island. (b) Comparison of the length-frequency distribution of 575 littleneck clams eaten by adult (open bars) and of 174 eaten by yearling (shaded bars) Northwestern Crows foraging in Well Bay.

with 29.0 ± 0.45 mm for adults (Fig. 3). A comparison of the length-frequency distributions of clams eaten by and rejected by yearlings (Fig. 4) provided evidence that they discriminate in choosing food items.

Duration of search and handling times.—Yearlings spent significantly more time than adults in every part of the search and handling process, except to fly from the drop zone back to the clam bed (Table 1). They also required an average of 2.0 (n = 153) drops to break open clams, significantly more than the 1.7 (n = 460) drops per clam required by adults (Mann-Whitney U-test, $0.05 > P > 0.01$). The number of drops made by both yearlings and adults to break a clam was independent of clam length (Richardson and Verbeek 1986), so this difference in adult and yearling performance was not simply the result of differences in diet breadth. The time it took an adult to remove the meat from a broken shell was an increasing function of clam length (Richardson and Ver-

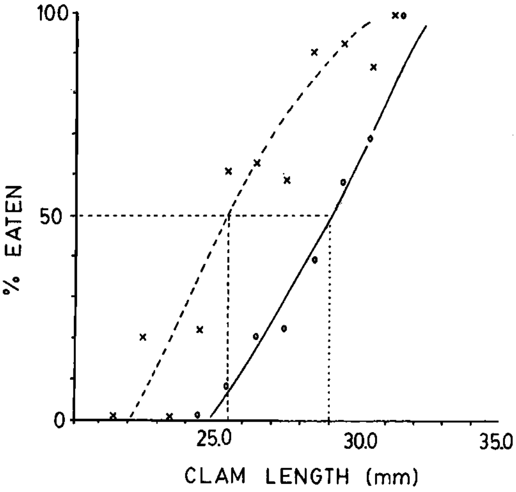

Fig. 3. The percentage of each size class of clam eaten by adult (circles) and yearling (crosses) crows. The level of 50% preference, assumed to represent the average yearling's choice of diet, is shown at 25.5 mm for yearlings and 29.0 mm for adults.

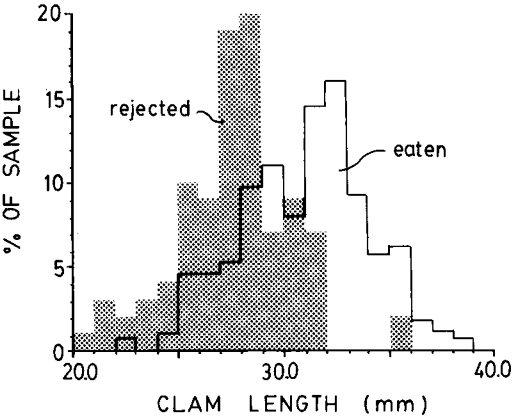

Fig. 4. Comparison of the length-frequency distribution of 174 littleneck clams eaten by and 98 clams rejected by yearling Northwestern Crows.

beek 1986), but there was no relationship (Kruskal-Wallis test, $P > 0.9$) between the meat extraction times of yearlings and clam length (Fig. 5). It is unlikely that extraction time would be constant over the whole range of lengths, especially for clams as small as 10 mm in length. The optimal diet for yearlings was calculated using both a constant extraction time of 48.7 s (the median observed time for yearlings) and a functional relationship between extraction time and length with the same exponent but with a small arbitrary increase in the y intercept observed for adults (Fig. 5). This second relationship gave an approximate fit to the data and was used to evaluate the effect on the predicted optimal diet of assuming some curvilinear relationship between extraction time and clam length. The predicted optimal diet was the same in both cases, and the form of this relationship was of relatively little consequence in our calculations. The net energetic worth of clams to both adults and yearlings was an increasing function of clam length, and diet breadth is therefore conveniently expressed as the smallest clams that should be in corporated into the diet.

The optimal, energy-maximizing diet.—The maximal net energy yield for a yearling, obtained from a diet containing clams of 25.0 mm and longer, is within 1.4 standard errors of the observed lower limit to the diet of 25.5 mm (Fig. 6). Agreement between the observed and predicted diet limits of yearling crows was similar to the agreement between the predicted limit of 29.0 mm and observed limited of 28.5 mm for adult crows (Richardson and Verbeek 1986). The yearlings' diet produced only approximately 13 J/s, however, considerably less than the maximum of 47 J/s obtained by adult crows from their optimal diet (Fig. 6).

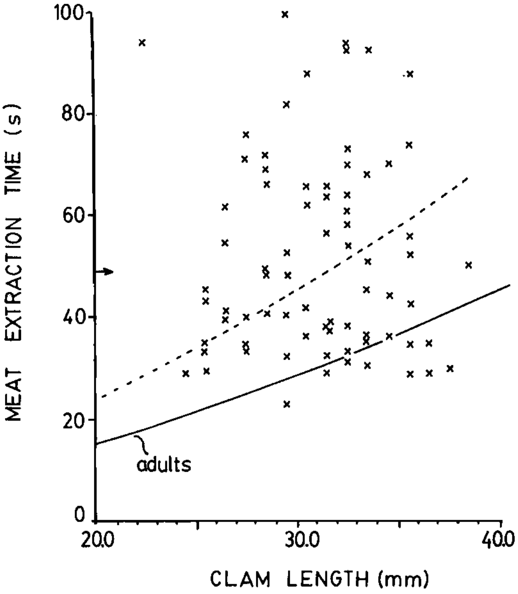

Fig. 5. The time for yearling crows to extract the meat from 76 littleneck clams ranging from 22 to 40 mm. The solid line indicates the observed relationship between clam size and the time for adults to extract the meat (Richardson and Verbeek 1986). The arrow indicates the median time of the 76 observations for yearlings, and the dotted line gives the arbitrary relationship used as an alternative to constant extraction time.

DISCUSSION

Sources of yearling inefficiency.—The most probable reason for the poor performance of yearling crows is that the complex foraging skills considered here can be learned only over time. Young birds follow their parents for the first few months after fledging, and initial learning is probably by observation and imitation. Refinement of the young birds' foraging skills after this period of parental association appears to be a process of trial and error. Some yearlings made flights similar to drop flights but without releasing the clams, others repeatedly and unsuccessfully dropped clams while standing on the ground, and others dropped

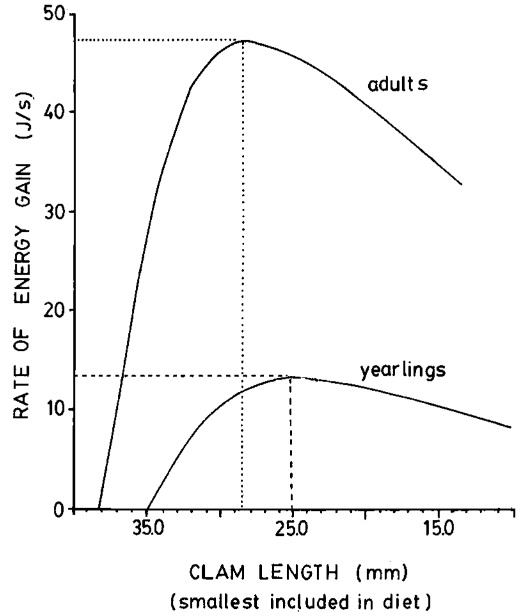

Fig. 6. Comparison of the rate of net energy gain of adult and yearling crows feeding on different size ranges of clams. Dotted lines indicate the optimal diet limits. Clams above this size should always be eaten when encountered.

TABLE 1. Mean duration (s) of search and handling times of adult and yearling Northwestern Crows feeding on littleneck clams.[a] Sample sizes are given in parentheses.

	Time	
Activity	Adults	Yearlings
Searching	34.6 ± 4.09 (186)	64.4 ± 5.93 (70)***
First drop	4.2 ± 0.54 (80)	6.1 ± 0.39 (74)**
Between drops	5.5 ± 0.55 (95)	8.8 ± 0.70 (64)***
Second drop	2.0 ± 0.24 (96)	3.0 ± 0.26 (66)*
Return flight	3.6 ± 0.27 (100)	3.7 ± 0.18 (68)

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

two clams simultaneously, a technique used by only one adult during the study.

There are other potential causes of yearling inefficiency besides inefficiency that results from the learning process. These include maturational blocks, the absence of an immediate need for nonbreeding birds to forage efficiently, and problems that may ensue in later skill learning from over-specialization as a juvenile (Olive 1982).

Common Crows (*Corvus brachyrhynchos*) and Northwestern Crows are close to adult mass when they fledge (Emlen 1936, Butler et al. 1984) and appear to achieve flight capabilities approaching those of adults within a few months of fledging. Consequently, as with other young birds (Barash et al. 1975, Maron 1982), the source of this juvenile inefficiency probably is not maturational. Another possibility is that the selective value of foraging optimally may be low for young that have attained adult size but have limited opportunity to breed. This would be true only if birds that performed submaximally as yearlings were equally proficient foragers at maturity as those that performed as well as their learning limitations would allow during their juvenile year. The high mortality of nestling crows on Mitlenatch, apparently from starvation (Richardson et al. 1985), suggests strong selective pressure for foraging efficiency, and this is most probably achieved by constant practice.

The final possibility discussed here is that inefficiency arises from the need to retain behavioral plasticity until reaching maturity. It may be maladaptive to become highly proficient at a specialized skill like dropping clams if this inhibits the development of efficiency in some other specialized skill later in life. If eventual reproductive success is not limited by food-gathering ability as a yearling, and if young crows are forced to disperse to areas containing different food types before establishing breeding territories, it may be beneficial for them to develop a wide foraging repertoire. The Northwestern Crows of Mitlenatch occupy the island only during the breeding season. They spend the rest of the year on Vancouver Island or one of the other small, forested islands nearby. The delayed and cooperative breeding exhibited by these birds (Verbeek and Butler 1981) suggests strong competition for mates, breeding sites (Brown 1974, 1978), or resources (Verbeek 1973). Many of the prey types eaten by crows are only locally abundant, and dispersal to avoid competition may take crows to sites where the necessary foraging techniques are different from those of their natal territory.

Diet selection.—Yearling crows selected a diet that maximized their net energy intake within the constraint of some obvious inefficiencies. The agreement between the observed and predicted diet limits for yearlings may have been accidental rather than the result of selective feeding. Diet selection by fledglings was largely directed by their parents, who initially cracked open clams and left them for the attendant young to remove the meat. Subsequently, the adults simply dug up clams and placed them in front of the young, who broke the clams themselves. At this stage, while still learning to dig for prey, the young also found and ate smaller clams that adult birds had rejected. This mixture of clams, intentionally and unintentionally presented to them, was similar to the size range that they took as independent yearlings. The mean size of clams rejected by the yearlings (Fig. 4), however, attests to the fact that they exercised some choice.

Diet selection could involve the integration of information from each of the component parts of the foraging process. Making the appropriate choices would then involve a greater degree of sophistication than simply learning to perform the component activities efficiently. If, by comparison, diet selection is made on the basis of some simple rule of thumb, there is little reason why the ability to make suitable choices should not develop, as it appears to do in this study, as rapidly as development of efficiency in other foraging activities.

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