A FIELD STUDY OF DIET SELECTION AND OPTIMIZATION BY NORTHWESTERN CROWS FEEDING ON CLAMS: TESTS AND PREDICTIONS

by

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A field study of diet selection by northwestern crows feeding on clams:
predictions and tests

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ABSTRACT

During April to August, 1979 to 1982 I investigated selective predation, foraging energetics and diet optimization by northwestern crows *Corvus caurinus* feeding on littleneck clams *Venerupis japonica*.

The intensity with which crows searched an area was not correlated with the ratio of large to small clams, nor was diet choice apparently influenced by changes in the size-frequency distribution of clams resulting from predation or growth. The crows' success per dig or probe was proportional to clam density and they also searched areas from which all clams had been experimentally removed. This suggested that the location of each dig or probe was random rather than in response to some stimulus associated with the presence of a clam.

A model was constructed to compensate for size related influences on the availability of clams: the maximum horizontal cross sectional area of the clams, the depth distribution of each size class of clam, and the shape and depth distribution of searches made by the crows.

From the size frequency distribution of live clams, the relative availability indices, and measured search and handling times, I calculated that the optimal diet consists of clams 28.5 mm and larger. Live clams measured from 10 to 42 mm, but the crows' diet, determined by collecting empty shells from clams which they had eaten, was restricted to those greater than 29.0 mm. By experimentally eliminating search costs, and then part of the handling costs, crows were induced to extend their diet to include clams as small as 22 and 14 mm, respectively. These values were also close to those predicted by the model in such circumstances.

Yearling crows were much less efficient than adults in finding and handling prey. They also fed on smaller clams (25 mm and larger), but in contrast to their otherwise inefficient performance, this extended diet was very close to their calculated optimum.

At tide levels of less than 2 m the crows fed preferentially on invertebrate prey from beds of *Ulva lactuca*. This diet yielded less than a quarter the rate of energy gain obtained by feeding on clams. Feeding on clams should provide sufficient energy to raise 4 young, yet an average of only 1 per nest was fledged. Most died, apparently of malnutrition, during the first 7 d after hatching, emphasizing the possibility of dietary constraints other than energy on the reproductive success of these birds.

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Finally, for sharing the fun of working in the field and the privations and tribulations of being a student, I thank my family; Nita, Robin and Tony.

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I. INTRODUCTION

The rules which a predator should adopt in choosing its diet from an array of possible prey types were first postulated by MacArthur and Pianka (1966) and Emlen (1966). Briefly, the predator should assess the net gain of energy, or some other suitable currency, per unit of handling time from eating each type, and rank them accordingly. Sequentially adding types of lower profitability (energy per time) to an existing diet will reduce the time and energy spent in searching but also lower the average rate of energy gained per capture. The optimal diet, which maximizes the rate of energy intake, will result when the benefit gained by adding another prey type to the diet is more than offset by the concomitant loss.

The great intuitive appeal of this optimization principle, and the apparent high testability of the hypotheses generated by it, has led to a large number of studies attempting to validate the underlying theory of diet selection. Despite this, after 15 years of effort, it could be asserted by Werner and Mittelbach (1981) that only three studies of naturally foraging predators (those of Belovsky 1978, Goss-Custard 1977a,b and Mittelbach 1981) had satisfactorily demonstrated selective feeding resulting in the consumption of the optimal diet.

The scarcity of convincing field studies can be attributed mainly to the complexity of the environments and behavioral patterns involved (Zach and Smith 1981). The difficulty of measuring, and sometimes even identifying, the parameters neccessary to predict the optimal diet has led many researchers to simply show that a predator feeds preferentially on the most profitable prey. However, as Sih (1982) and Zach and Smith (1981) have pointed out, such results do not neccessarily constitute evidence of optimization. In addition, studies showing selective feeding may have a second, more serious, and less frequently confronted weakness: that of determining the 'availability' of each prey type to the predator. As an extreme example, using pit traps during the day is a totally inappropriate method for determining the prey available to a nocturnal, aerial insectivore. Sampling must be spatially and temporally congruent with the predator's foraging and must employ methods consistent with, or which can at least be corrected to reflect, those of the predator. Too few studies attempt to assess the suitability of the sampling methods used.

Given these difficulties, why persist with field studies of diet selection and optimization? Smith (1978) expressed the opinion that the purpose of optimization studies is not to show that animals can optimize but to better understand the diversity of life. This understanding will not be accomplished by asking only what animals are capable of but also what they actually do in their natural environments. With this in mind, the aim of this study was to examine the foraging behavior of a predator in a natural situation that was neither unrealistically simple nor intractably complicated. The Japanese littleneck clam (Venerupis japonica) is an important part of the diet of northwestern crows (Corvus caurinus) living on Mitlenatch Island, British Columbia, and for a variety of reasons, which are enumerated in Chapter VII, this provided an excellent system for the achievement of my aims. The body of this thesis is divided into 4 main sections:

1. a brief description of the study area, the predator and the prey (Chaps. II, III and IV);
2. a determination of the relative numbers of different sizes of clams available to foraging crows. This includes a description of the spatial and temporal distributions of my sampling and a comparison with the relevant distributions of search effort by the crows (Chap. V). It also includes a demonstration of the methods by which the crows probably locate buried clams. Correction factors are then generated to reflect size specific differences in the detectability of clams to crow and human searching methods (Chap. VI),
3. a determination of the actual diet range of crows feeding in Well Bay. The potential net energy gain from all possible diet breadths is calculated and compared with the energy yields from the observed diet (Chap. VII). The performances of adult and juvenile birds are then compared (Chap. VIII);
4. an evaluation of the crows′ utilization of clams as a food source relative to some other potential sources. Estimates of the potential energy gain from each source are made. The prediction of a preference for the most energetically rewarding source is compared with the birds′ observed

preference. The estimated energy gains are also compared with the predicted energy demands of other activities, particularly reproduction (Chap. IX).

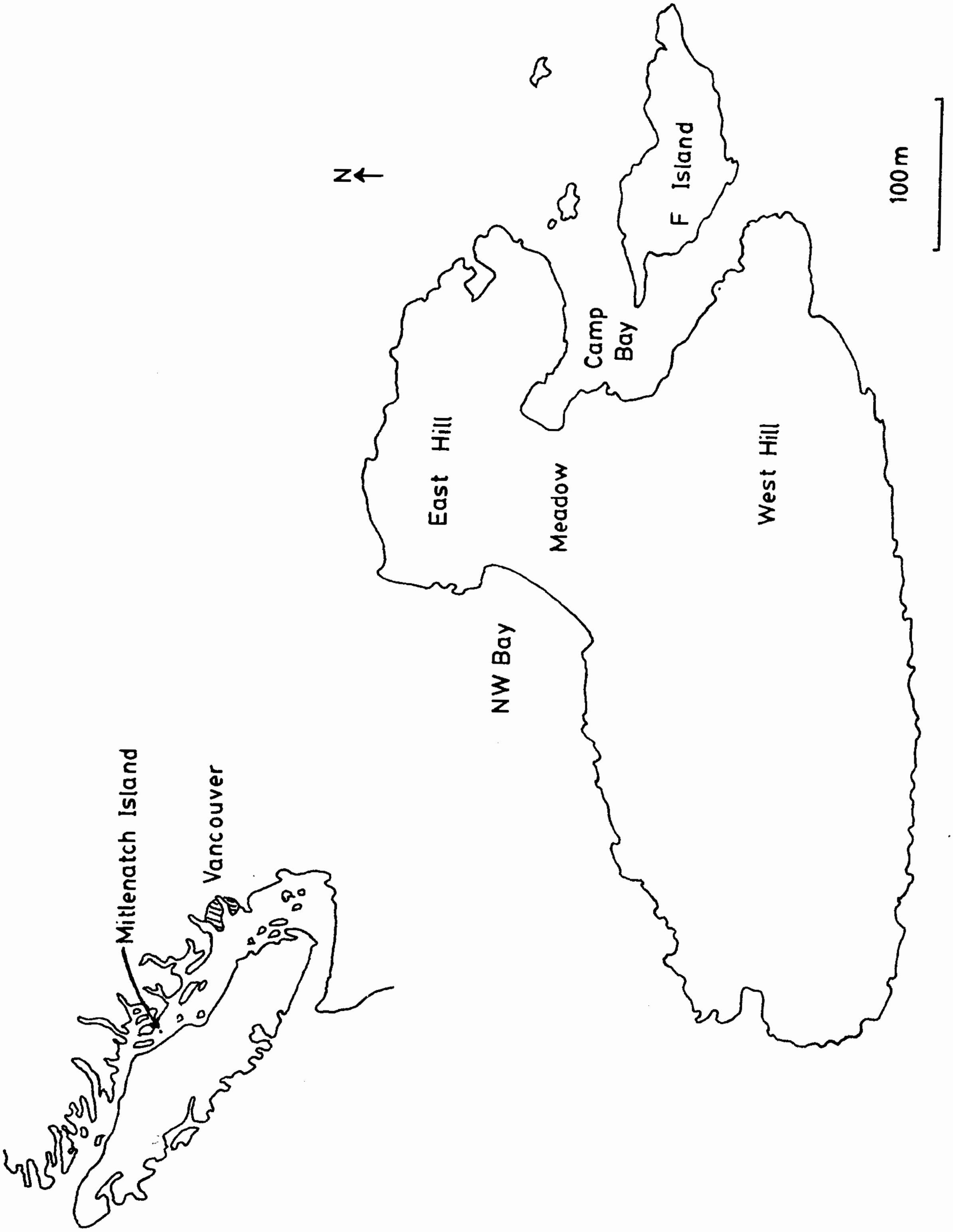
Each of the main chapters has been written in the form of a paper, with its own introduction, methods, results and conclusions. I felt that using this format, although it introduced a small amount of repetition, results in a clearer presentation of my research.

II. STUDY AREA

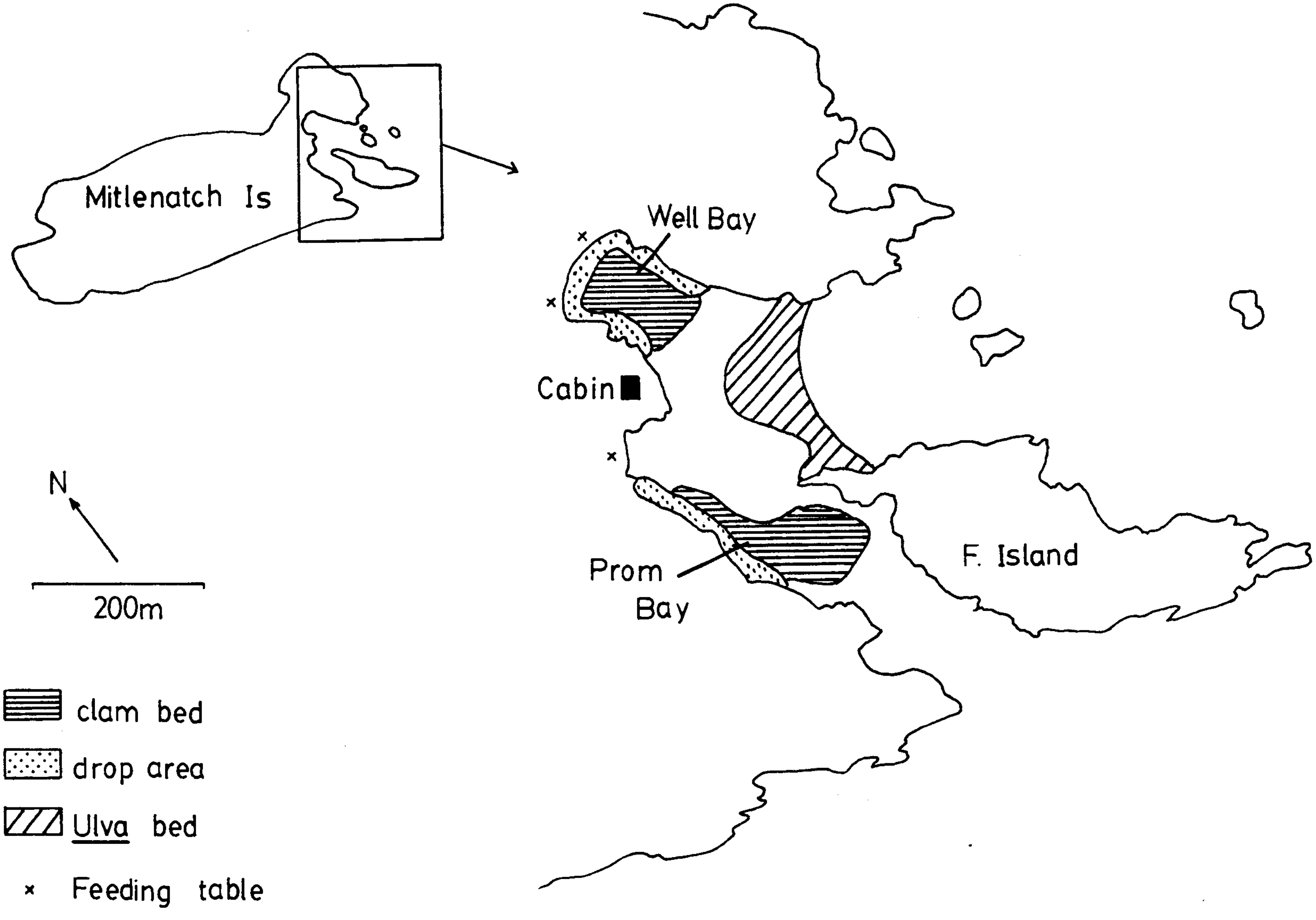
All observations were made on Mitlenatch Island, British Columbia (49 57′ N, 125 00′ W), a 35 ha island at the northwest end of the Strait of Georgia (Map 1). The nearest land is Hernando Island, 5 km to the northeast. Vancouver Island, which seems to offer the best alternative feeding and breeding habitat, is 11 km to the southwest. Although crows do travel to other islands, the distances involved probably make frequent use of the resources available there prohibitive. Topographically, Mitlenatch Island consists of two low (< 60 m) rocky hills separated by a grassy meadow. Bordering this to the south, and lying between shoulders of the two hills, is Camp Bay (Map 2). This contains the only extensive area of intertidal beach on the island. A number of bays and other features within Camp Bay have been popularly identified and are shown in Map 2.

Well Bay has a gently sloping beach of mud and fine gravel, irregularly covered by stones and boulders. In some areas these have been completely cleared for use in the construction of fish traps. These traps and any remaining stones served as useful reference points and were used in constructing an accurate map on which to plot the location of clams and the activities of the crows.

Map 1. Map of Mitlenatch Island showing the major topographical features. Inset is a map of the southwest coast of British Columbia to show the location of Mitlenatch Island.


N
F Island
100m
Camp Bay
East Hill
Meadow
West Hill
NW Bay
Mitlenatch Island
Vancouver

Map 2. Map of the major features of Mitlenatch Island mentioned in the text.


Mitlenatch Is
Well Bay
Cabin
Prom Bay
F. Island
N
200m
clam bed
drop area
Ulva bed
× Feeding table

Prom Bay is considerably less homogeneous than Well Bay, with a substrate of crushed shells, gravel or large stones. Patches of oysters (Crassostrea gigas), mussels (Mytilus edulis), assorted brown algae and standing water are irregularly distributed over the surface. Therefore, although littleneck clams were plentiful in both bays, data collection was concentrated in Well Bay because of its greater substrate homogeneity. Most of Camp Bay is surrounded by a rocky shelf. When crows find a clam, they fly to drop and break it open on this rocky shelf. The areas most frequently used I refer to as the drop areas (Map 2).

Lower in the intertidal are beds of Ulva, extending up the beach from about the 0 m tide level. The upper extension and the percent cover of the Ulva varies, but generally declines through the course of the summer as the seaweed becomes dessicated or is torn loose by storms. A variety of invertebrates and small fish found in the Ulva constitute the only alternative to clams as food in the beach area.

III. THE CROWS

Approximately 60 pairs of crows breed on the island, but the absence of a reliable winter food source (Chap. IX) makes it unlikely that they are resident throughout the year. During a 3 day visit in November 1980 no crows were observed on the island. In late March 1981 crows visited the island only during the day, gathering in their normal summer roost shortly before dusk and then flying to Vancouver Island. Winters are probably spent close to the nearby urban centres on Vancouver Island. In addition to the breeding birds, an indeterminate and probably fluctuating number of yearlings and non-breeders also spend part of the summer on the island. The total summer population is probably between 150 and 200 birds. Butler (1980) outlined the breeding chronology of the crows and identified shellfish as one of their major food sources. Zach (1978,1979) gave details of the methods used by crows in handling molluscan prey and showed that the birds made energetically appropriate choices in dealing with them. He also showed that the crows were apparently size selective, favoring large whelks *Thais lamellosa* over small ones.

A small proportion of the breeding birds maintain territories contiguous with the Camp Bay intertidal area. These birds are often dominant over others on parts of the beach close to their territory but intruder pressure probably prevents them from maintaining exclusive use of the beach. The remainder of the birds nest in trees and bushes at varying distances from the beach. From observations of individually banded birds and the directions of travel to and from the beach, it is evident that birds from all parts of the island forage in the clam beds and move freely from one beach to another. Some birds also use areas of the meadows adjacent to the beach as short-term caches for clams and other items captured in the inter-tidal (James 1979, James and Verbeek 1983).

Crows have no natural predators resident on the island. Compared to the glaucous-winged gulls (Larus glaucescens) they respond little to the bald eagles (Haliaeetus leucocephalus) which frequently hunt over the island. There is also suprisingly little kleptoparasitism by either gulls or other crows (pers. obs.) and the influence of inter- and intra-specific interference on feeding behavior seems to be minimal.

IV. THE CLAMS

Japanese littleneck or Manila clams (Venerupis japonica Deshayes), also known as Tapes philippinarum (Adams and Reeve), were introduced to British Columbia around 1936 as accidental inclusions in imported oyster seed. Their rapid spread (Neave 1944) was attributed to the fact that they did not compete for space with the most similar native species Protothaca staminea and Saxidomus giganteus (Quayle and Bourne 1972). In Camp Bay Saxidomus is found lower in the intertidal than Venerupis and although there is considerable horizontal overlap between Protothaca and Venerupis, the former are usually deeper below the surface (pers. obs.) In Well Bay Protothaca constitutes approximately 11% of the clams present, yet represents less than 3% of the clams eaten by the crows (pers. obs). I show later that Japanese littleneck clams are almost sessile, being incapable of the rapid burrowing used by other species of clam to escape predation. Schmidt and Warme (1969) report that Protothaca moved on the beach surface by rocking back and forth on their foot, leaving V section trails. Such movements are not universal (Paul and Feder 1973) and no signs of surface movement were observed in Camp Bay. This study was therefore free of the problems, so graphically illustrated by Myers et al. (1980), that arise from short term changes in prey distribution.

V. SAMPLING AND THE PERCEPTION OF PREY AVAILABILITY

INTRODUCTION

A major problem in showing selective feeding by predators in natural environments, is to realistically assess the availability of each prey type. The sampling methods of the predator are determined by its morphology, while scientists have a wide array of techniques and equipment at their disposal. Conversely, foraging may occupy the bulk of a predator's time, while researchers are frequently constrained by other demands and must restrict their sampling to selected times and areas. Such differences in sampling techniques may result in different perceptions of how many of each size class are available. The optimal diet for a predator is determined by its encounter rate with high quality prey. Frequent encounters should result in a diet consisting only of those types, while if such prey are more scarce, the maximum energy intake will be achieved by including some of the less profitable size classes in the diet (MacArthur and Pianka 1966, Schoener 1971, Werner and Hall 1974, Krebs 1978). Hence, in predicting the optimal diet for an animal, it is essential to estimate how many of each prey type the predator perceives to be present rather than how many there actually are.

The purpose of this chapter is to compare the spatial and temporal distributions of sampling by crows and myself, and to assess the extent to which any differences between them may influence predictions of what constitutes the optimal diet.

Paul and Feder (1973) found that small *Protothaca staminea* in Galena Bay, Alaska, were generally lower in the intertidal area than larger individuals. Crows may be sensitive to size related differences in spatial distribution of their prey and search accordingly, concentrating on those areas which contain high proportions of large clams. This sampling method would result in a higher proportion of large clams in their sample than in an unweighted, random sample.

The calculations of optimal diets for adult and yearling crows in Chapters VII and VIII assume a stable size frequency distribution. During the course of a protracted period of observation both growth and mortality could change the size-frequency distribution of the prey. The growth of small clams to a size which the crows normally eat may result in an increase in the density of preferred prey. Conversely, the birds' predation could result in a significant depletion of large clams (O'Connor and Brown 1977), and a broadening of diet width. Also, recruitment to shellfish populations is known to be very variable (Paul and Feder 1973). Since I collected data over a period of 4 y, annual changes in the clam population structure could have resulted in a different predicted optimal diet for each year.

METHODS

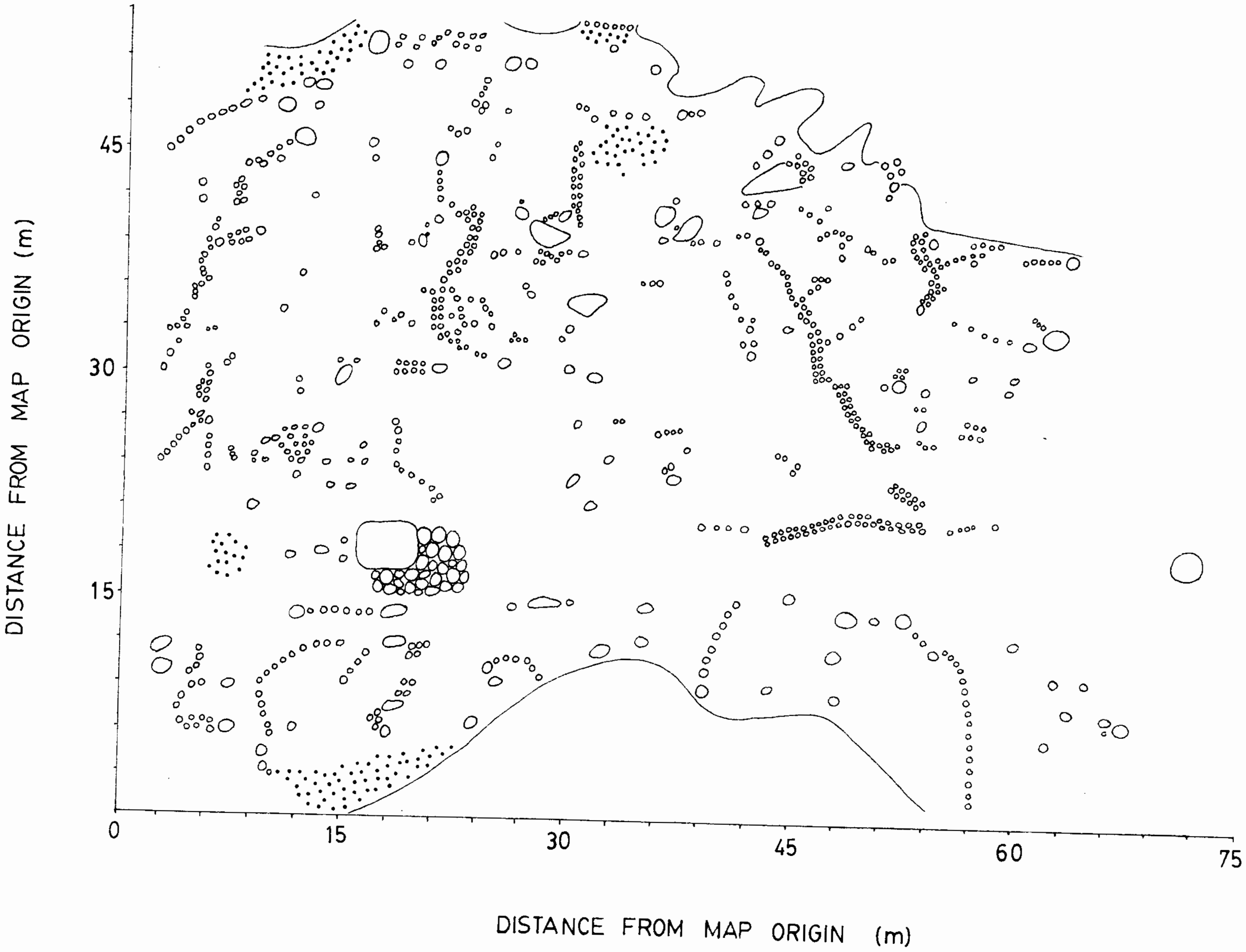
The data were collected between mid-April and mid-August of 1979, 1980 and 1981 in Well Bay, Mitlenatch Island (Map 2). I first constructed a large scale map of the beach on which to plot data (Map 3). Two prominent boulders were used to establish a base line and the beach was marked out in a regular 3 by 3 m grid. This grid was used to determine map coordinates for stones and the remains of the fish traps. All other figures involving spatial distributions are based on this same grid system.

Spatial distribution of sampling

In 1979 and 1980 I sampled one hundred and seven 25 by 25 cm quadrats at randomly determined map coordinates. In 1981 a more accurate determination of the spatial distribution of clams was made using 202 quadrats located regularly, at 3 m intervals, over the whole clam bed. I removed the substrate from each quadrat to a depth of 15 cm. This material was placed in a bowl and sorted through by hand. The greatest overall shell length (Fig. 1) of all the clams found in each sample was measured with vernier calipers. Clam size is expressed as the greatest overall length throughout this thesis.

The crows were presumed to sample as they searched, with each clam detected, whether eaten or not, adding to their

Map 3. Large scale map of the Well Bay clam bed. The prominent boulders at coordinates 18,18 and 72,18 were used as standard reference points for the construction of the map. Solid lines indicate the rock margins of the beach and stippling, areas of complete pebble cover. The 'circles' mark the positions of identifiable boulders and clumps of boulders. The regular linear arrangements of stones are the remains of indian fish traps. The coordinate system is based on a 3 m square grid and all subsequent diagrams of this beach are based on the same system.


45
30
15
DISTANCE FROM MAP ORIGIN (m)
0
15
30
45
60
75
DISTANCE FROM MAP ORIGIN (m)

15b

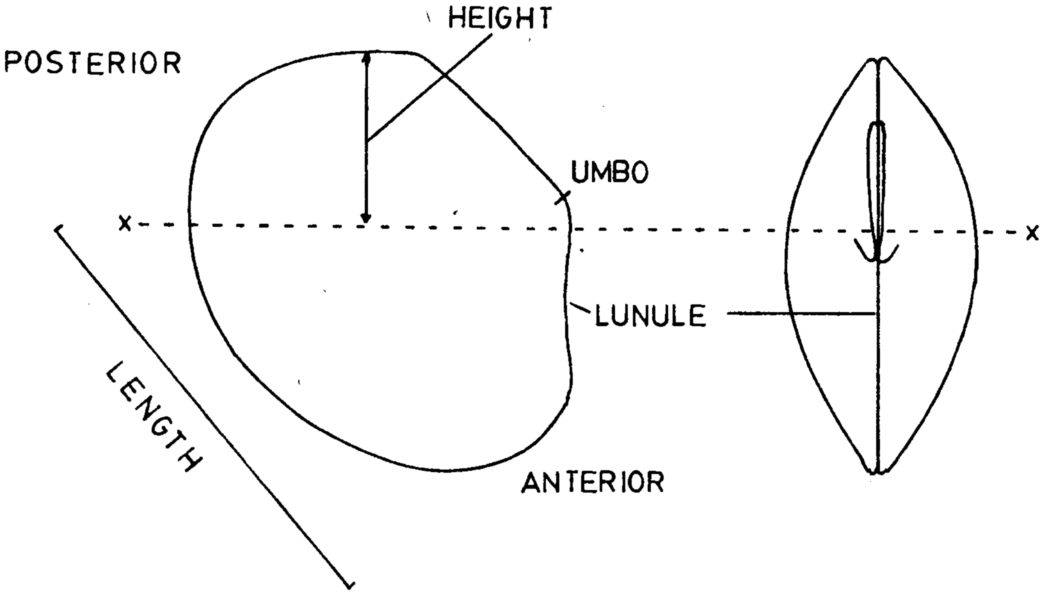


Fig. 1. Schematic representation of the orientation of clams in the beach and the physical parameters used in the calculation of availability indices. x----x marks the plane of the plan area. The margin of the shell between the umbo and the anterior end is normally perpendicular to the beach surface.

information about the size frequency distribution and total density of the prey. A single search consisted of either a probe (a single thrust of the bill to the surface or into the beach substrate) or a dig (a series of lateral swipes of the bill directed at the same spot on the beach). Search intensity was measured as the number of individual searches made by crows in each 3 by 3 m grid square during twenty, 2 h periods at different times and tide heights in May 1980. I waited for a bird to land on the beach, then marked each dig and probe made on the map. Because the volume of substrate searched by a dig was greater than that searched by a probe, the two methods were analyzed separately.

Temporal distribution of sampling

Although I sampled the clam population more intensely in some years than others, within each field season the sampling was distributed as evenly as the vagaries of the tide would allow.

Temporal variations in the crows′ utilization of the clam beds as a food source were determined by collecting and measuring all empty clam shells from the drop areas at intervals of approximately 3 days.

The influence of growth and mortality on the size-frequency distribution was determined by measuring all the clams in a 1 m^2 plot in late April 1980, replacing them, and measuring them again in late July 1980.

RESULTS AND DISCUSSION

Spatial distributions of sampling

Observation of the crows clearly showed that they do not search all parts of the clam bed with equal intensity (Figs. 2 and 3). Two factors apparently influenced their searching. Firstly, they foraged more in the portion of the clam bed highest up the beach, simply because it was exposed longer. More importantly, there was a significant relationship between the number of probes and digs made in an area and the density of clams (Fig. 4, Tables 1 and 2). Since the frequency with which crows searched different parts of the beach was known (Figs. 2 and 3), it would have been theoretically possible, but practically tedious, to derive a size-frequency distribution weighted to reflect their sampling methods. However, in the absence of any significant relationship between search intensity and the ratio of large to small clams present (Tables 3 and 4), the crows′ distribution of search effort will not alter their relative encounter rates with large and small clams.

Temporal distributions of sampling

There was a noticeable change in the size-frequency distribution of clams between April and July (Fig. 5). The modal size of first year clams increased from 15 to 18 mm and that for

Table 1. Relationship between the number of probes made in a 3 by 3 m square and the number of clams in a 25 by 25 cm quadrat located at the centre of the square. Each square corresponds with one of the grid squares of Map 3.

Number of	Number of clams per 25 by 25 cm quadrat				
probes	0	1-14	15-29	≥30	Total
0	11	34	9	1	55
1-9	13	32	10	6	61
≥10	4	11	16	15	46

$X^2 = 35.0$, df = 6, $p < .001$

Table 2. Relationship between the number of digs made in a 3 by 3 m square and the number of clams in a 25 by 25 cm quadrat located at the centre of the square. Each square corresponds with one of the grid squares of Map 3.

Number of	Number of clams per 25 by 25 cm quadrat			
digs	0-14	15-29	≥30	Total
0	35	6	1	42
1-4	36	14	7	57
5-9	20	8	8	36
≥10	13	8	6	27

$X^2 = 13.6$, df = 4, $.01 < p < .05$

Table 3. Relationship between the number of probes made in a 3 by 3 m square and the ratio of large (> 25 mm) to small clams in a 25 by 25 cm quadrat located at the centre of the square. Each square corresponds with one of the grid squares of Map 3.

Ratio of large/	Number of probes per 3 by 3 m square				
small clams	0	1-9	10-19	>20	Total
>1	28	26	17	15	86
<1	23	28	6	6	63

$X^2 = 6.29$, df = 3, $.1 > p > .05$

Table 4. Relationship between the number of digs made in a 3 by 3 m square and the ratio of large (> 25 mm) to small clams in a 25 by 25 cm quadrat located at the centre of the square. Each square corresponds with one of the grid squares of Map 3.

Ratio of large/	Number of digs per 3 by 3 m square					
small clams	0	1-4	5-9	10-14	>15	Total
>1	16	34	18	12	6	86
<1	22	16	15	5	5	63

$X^2 = 7.21$, df = 4, $.2 > p > .1$

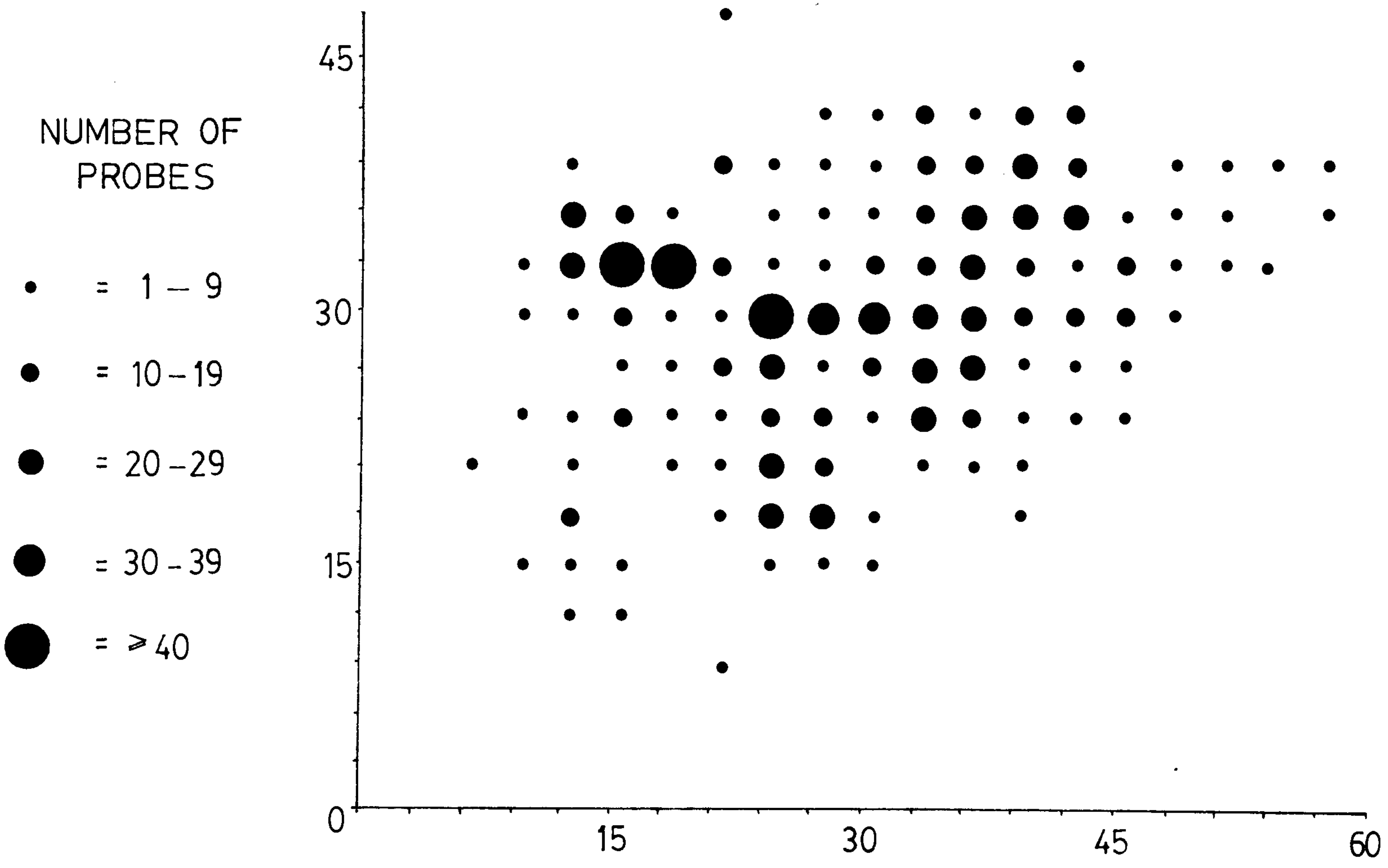


Fig. 2. Spatial distribution of 1133 probes made by northwestern crows searching for littleneck clams in Well Bay. The size of each dot is proportional to the number of probes observed in a 3 by 3 m square during twenty, 2 h observation periods in May, 1980.

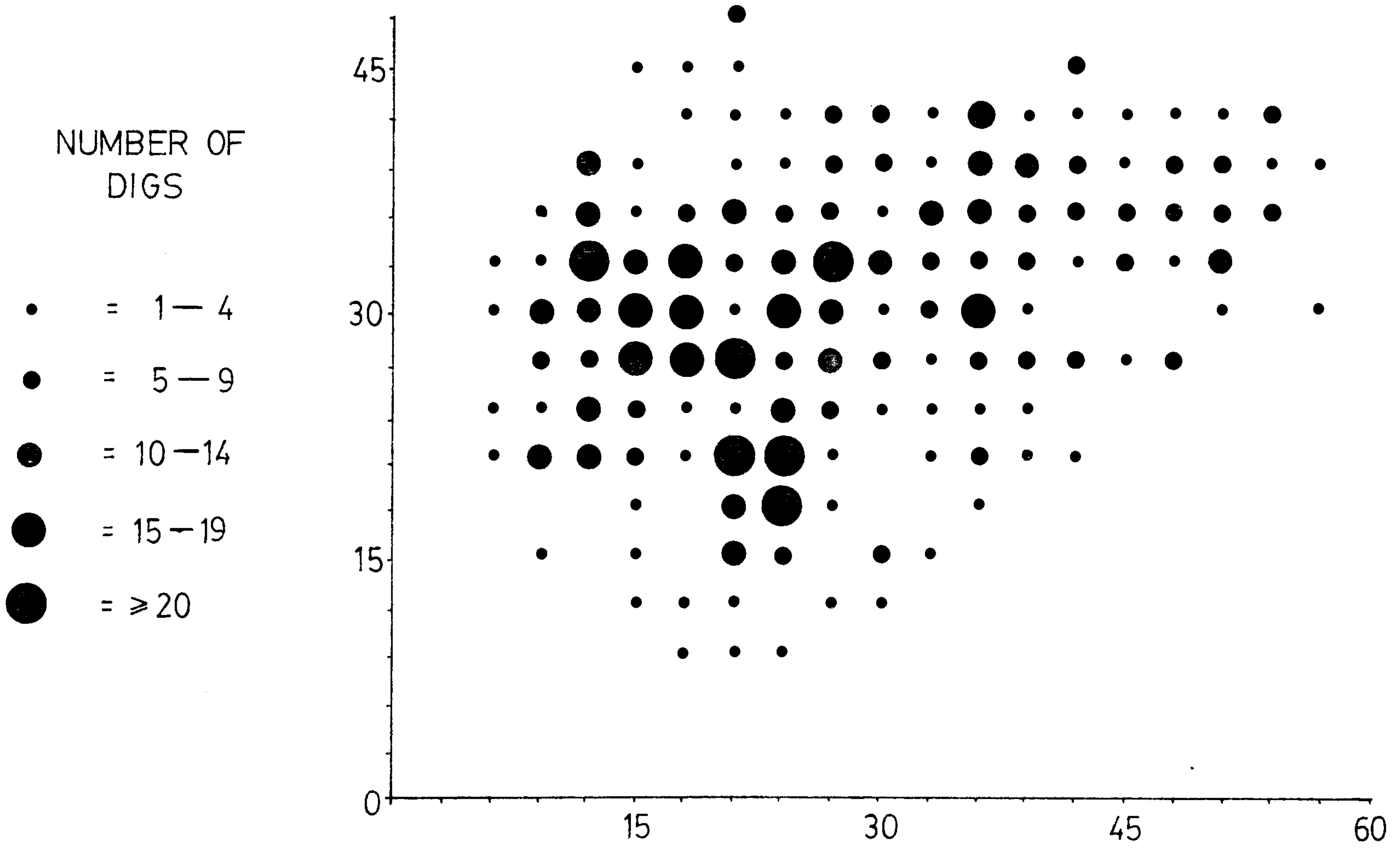


Fig. 3. Spatial distribution of 927 digs made by northwestern crows searching for littleneck clams in Well Bay. The size of each dot is proportional to the number of digs observed in a 3 by 3 m square during twenty, 2 h observation periods in May, 1980.

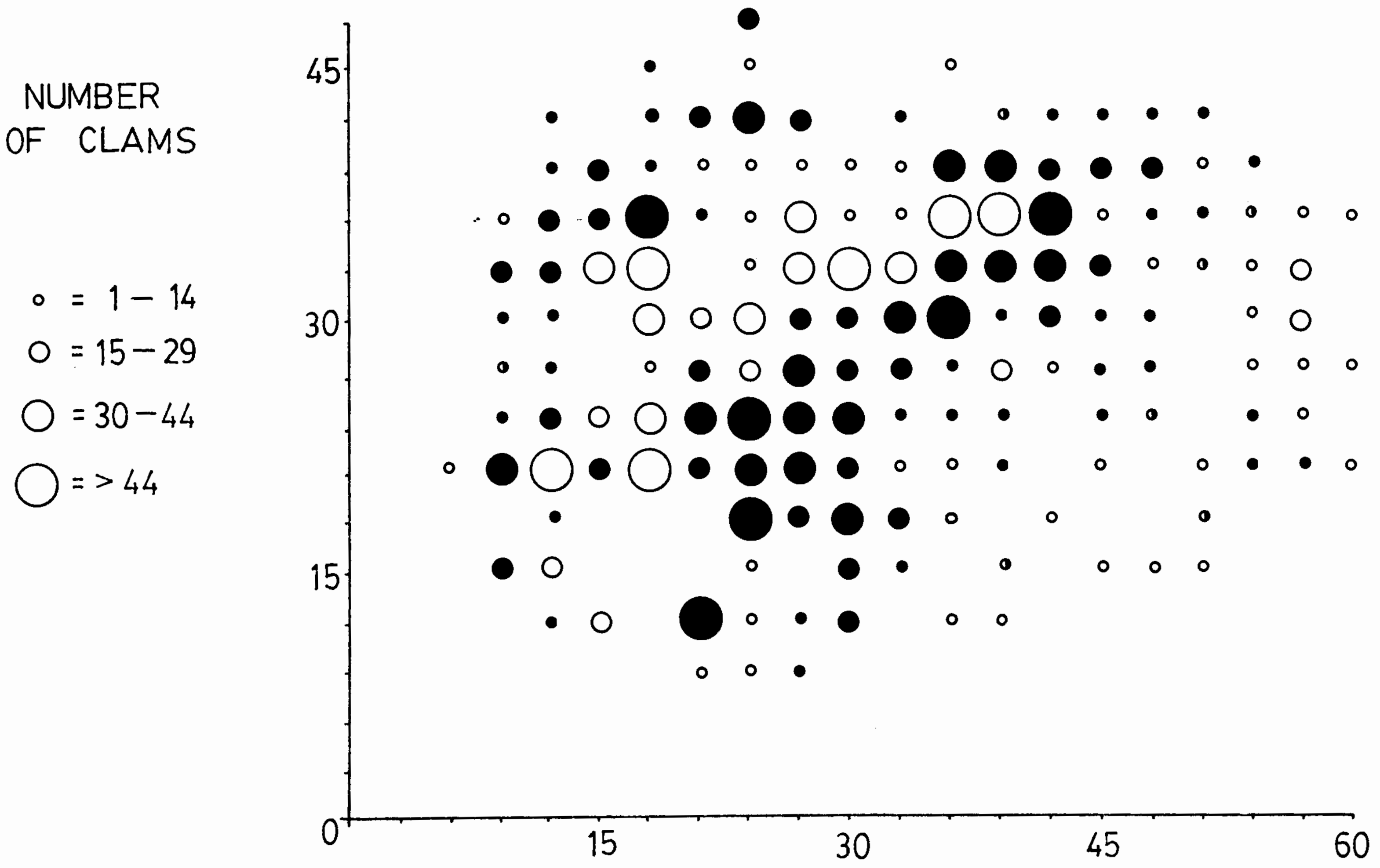


Fig. 4. Spatial distribution of clams in Well Bay. Each dot represents the location of a 25 by 25 cm quadrat and the size of the dot is proportional to the number of clams found in the quadrat. Quadrats in which there were more large (> 25 mm) clams than small ones are shown by open circles. Those with more small then large clams, by open circles.

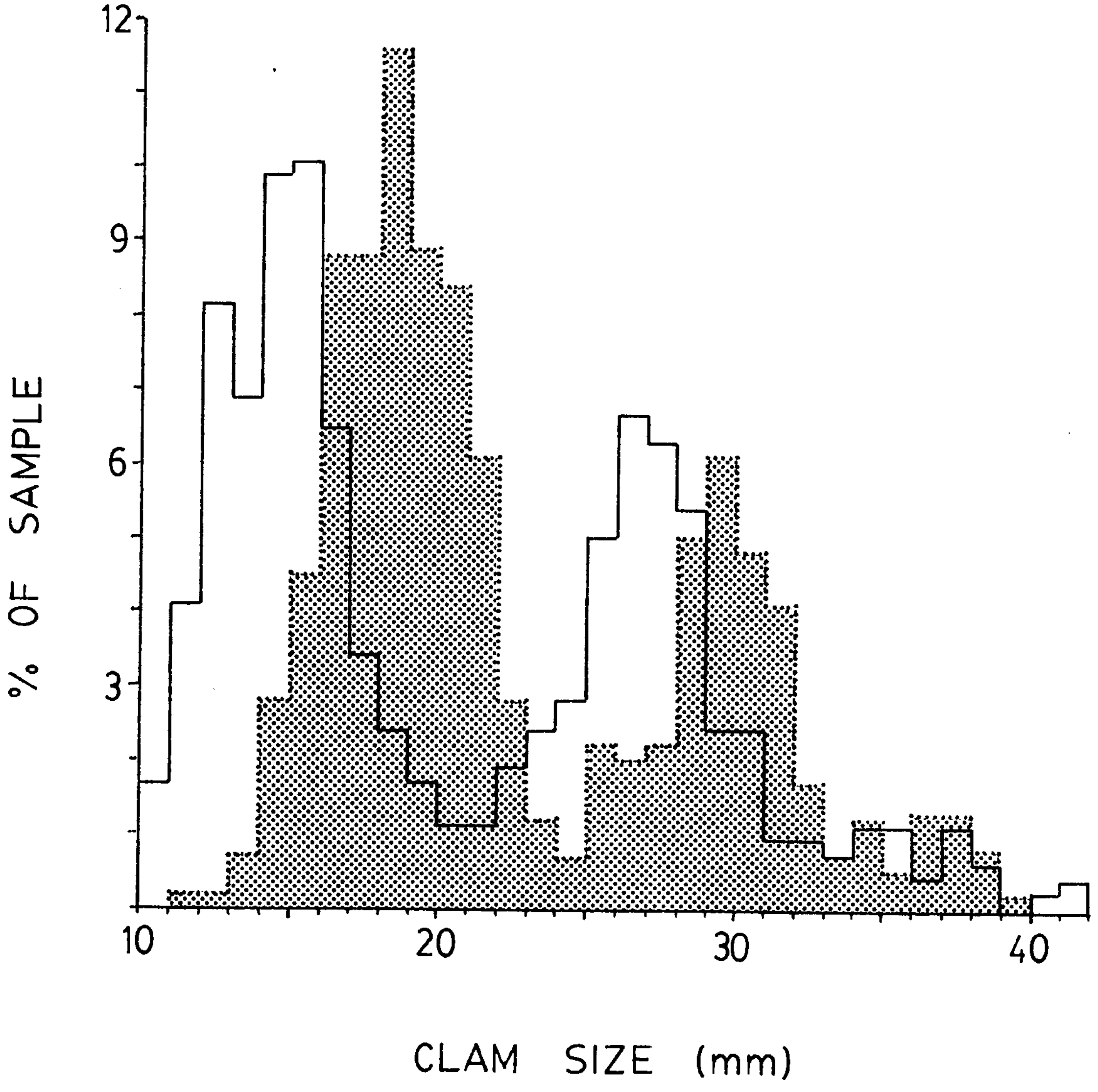


Fig. 5. Change in the size-frequency distribution of clams due to growth over a 3 mo period. Clams from a 1 m^2 plot were measured on 24.iv.1980 (——) and again on 27.vii.1980 (.....).

second year clams from 26 to 29 mm. Counter to this tendency for the density of larger clams to increase because of growth, the number of clams > 25 mm decreased by 4.7% (192 to 183) over the 3 mo period. This decrease is most probably due to crow predation. This level of loss due to predation was confirmed by the daily shell collections. The median number collected per day in 1980 and 1982 was 79 and 86, respectively. Researching the drop zones immediately after suggested a search efficiency of approximately 80%. Thus, the average daily consumption was about 100 clams, or 9,000 over 3 mo. The regularly spaced 25 by 25 cm quadrats sampled 1/144 th of the clam bed and yielded just over 1000 clams larger than 25 mm giving a total population of large clams of 144,000. The crows′ predation therefore amounted to a loss of about 6.3% over a 3 mo period. Such losses were presumed to have a minimal effect on the crows′ choice of diet.

Although there were ten-fold differences in the daily consumption of clams (Fig. 6), these were short term variations apparently linked with the tidal cycle. A regression analysis of the number of clams taken showed no significant change in the period over which the collections were made. Because the temporal distribution of my sampling roughly paralleled that of the crows, it is assumed that we had parallel perceptions of the size-frequency distribution of the clams.

Any seasonal fluctuations in prey density should produce fluctuations in the diet and in predictions of what constitutes the optimal diet. However, the constancy of predation and the

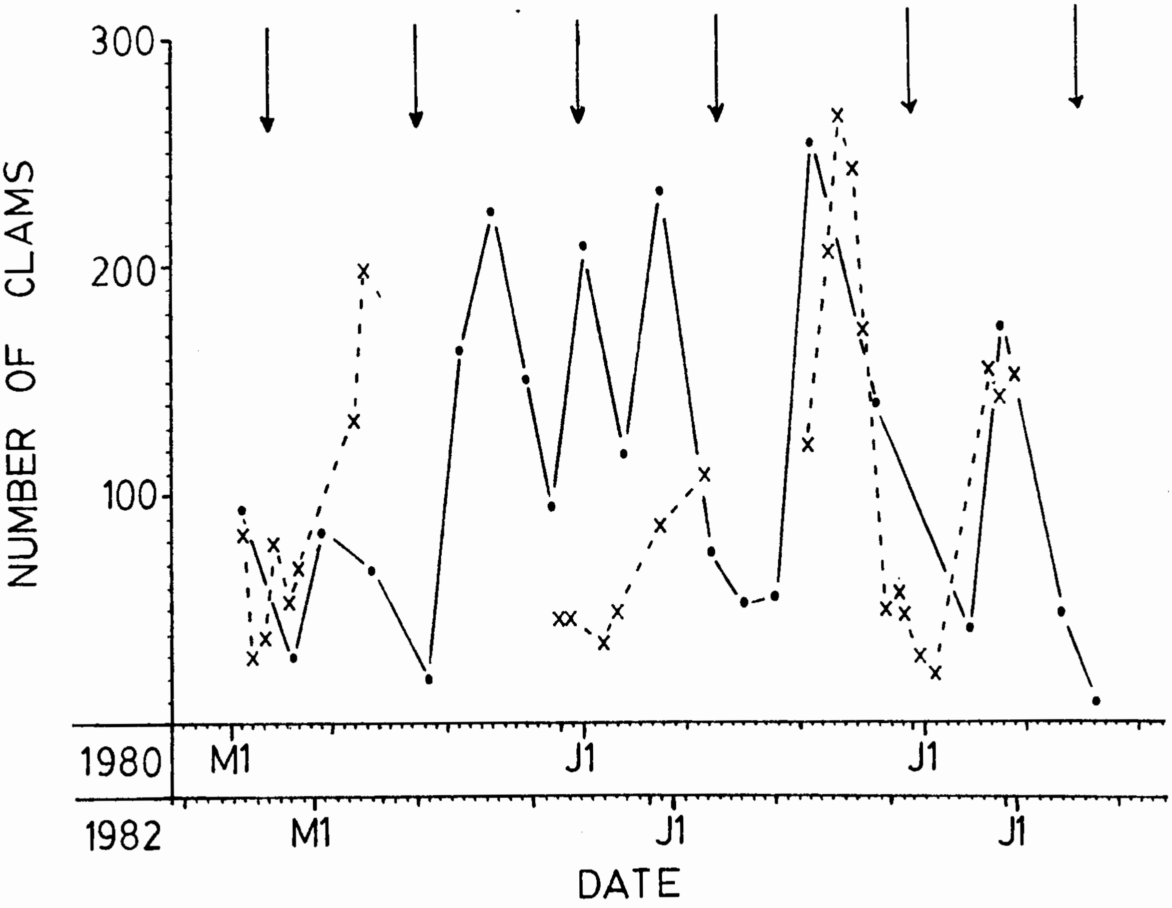


Fig. 6. The number of clam shells collected per day from the Well Bay drop zone. Collections were made shortly before the drop zones were covered by the tide and included only shells with some meat still stuck to them. The tide cycles in the 2 y were 6 d out of phase so the date axis for 1982 has been displaced to make the monthly high spring tides of each year coincide. Arrows indicate the date of spring low tides.

counteracting effects of predation and growth on the size-frequency distribution, make the prediction of a single yearly optimum for the crows' diet a valid objective.

Yearly variations in recruitment

It is evident from Fig. 7 that annual recruitment is highly variable. However, the important factor in diet selection is the density of preferred prey types. Radical differences in recruitment, as observed between 1980 and 1981, probably resulted in only slight changes in the overall density of large clams. The largest clams in this bed were 5 or 6 y old, while the smallest taken by the crows were only 2 y old. Only if there were a series of bad years, or some other non-age specific source of mortality, would the total density of clams 2 y and older be greatly reduced. Alternating years of high and low recruitment would average the density fluctuations for large clams. In fact, there was no significant difference (Kruskal-Wallis test, $0.1 > P > 0.05$) in the average number of clams larger than 25 mm per sample quadrat in 1979, 1980 and 1981 (5.3, 5.2 and 5.9 respectively). The absence of yearly differences in search times, the constant size range taken and the similarity in the numbers taken per day in 1980 and 1982, all support the contention that the population density of the clams was relatively constant. Despite this, because of these large, yearly variations in population structure, optimal diets were only calculated when the size-frequency distributions of both live clams and clams eaten by crows, and search times were measured in the same year. Handling times were assumed to be constant from year to year.

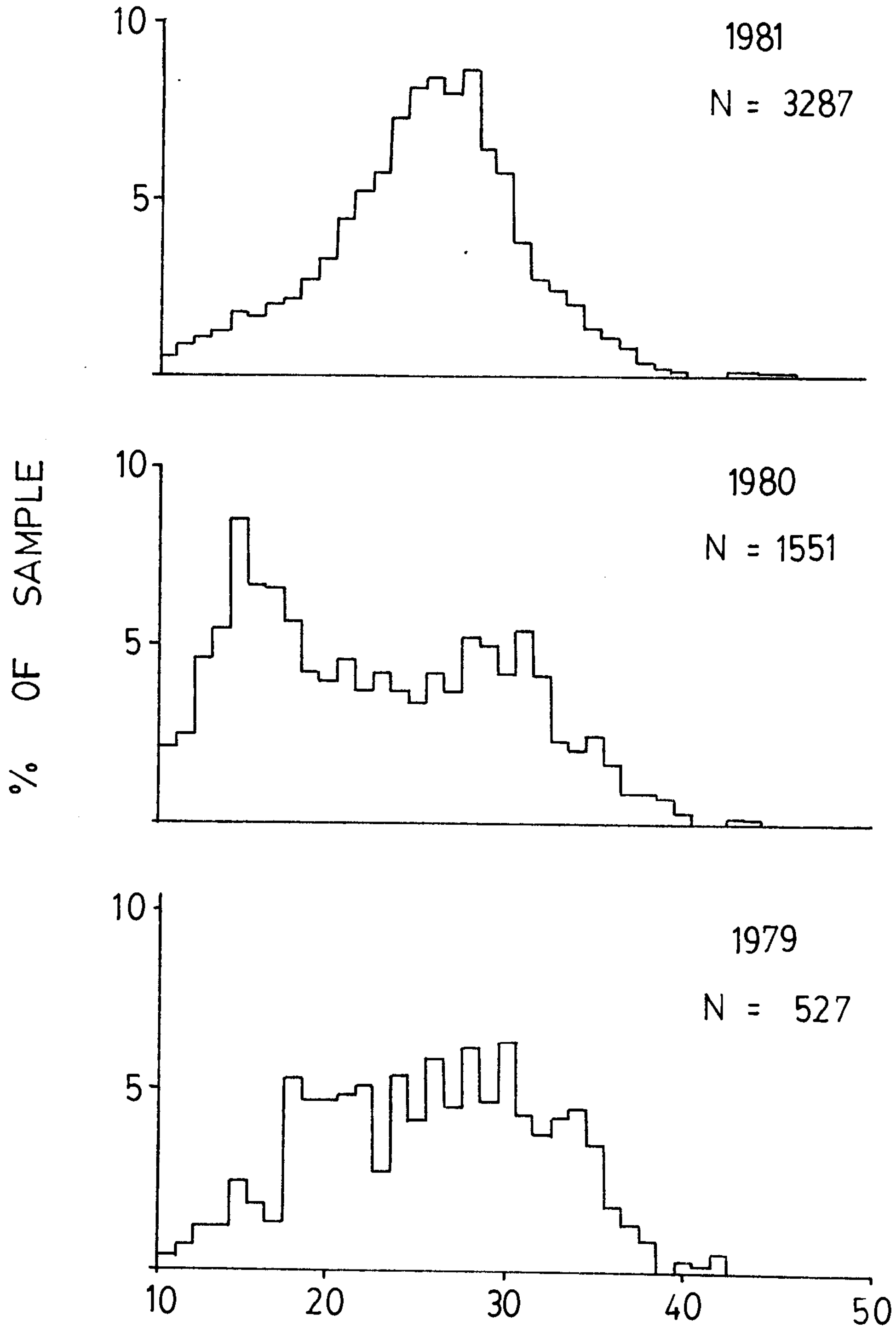


Fig. 7. Comparison of the size-frequency distributions of littleneck clams collected in Well Bay during the field seasons of 1979, 1980 and 1981.

VI. SEARCHING METHODS AND SIZE-SPECIFIC AVAILABILITY

INTRODUCTION

Current theories of foraging behavior suggest that a predator should feed selectively on that sub-set of potential prey types which provides it with the maximum intake rate of some dietary component(s) (Krebs 1978, Pyke *et al*. 1977). However, selectivity is difficult to demonstrate. The consumption of a greater proportion of one type of prey than another is not itself an indication of selectivity; that type may simply be easier for the predator to detect. Although the application of optimal foraging theories to complex situations has been questioned (Schluter 1981, Zach and Smith 1981), any alternatives will inevitably involve comparison between the proportion of a prey type in the diet and the rate at which it is encountered in the environment, relative to the other prey types. Thus the validity of tests of any foraging theory, current or future, will depend on the researcher's ability to distinguish between preferential consumption and differential availability. Availability is used here as a proportionality term relating the density of a prey in the environment to that detected by the predator. Detection of prey will be a function of the predators' search methods and the properties of the prey which make them vulnerable to those methods. The practical difficulties of measuring relative availabilities of different prey to an avian predator have been graphically illustrated by Myers _et al_. (1980) and Zach and Smith (1981).

The purpose of this chapter is to determine the relative availability of different size classes of the littleneck clam _Venerupis japonica_ to foraging northwestern crows (_Corvus caurinus_). Such a determination is seen as a prerequisite to further work on diet selection. For simplicity I have presented the argument in five sections.

1. Establishment of the search strategy used by the crows.
2. Development of a simple model, based on that strategy, to calculate availability indices for each size of clam.
3. Measurement of the relevant parameters of the crows' foraging techniques.
4. Measurement of the parameters of the clam population pertinent to those techniques.
5. Predictions and tests of the model.

SEARCHING STRATEGIES

When crows are foraging for clams they walk across the beach, pausing at intervals to search in the substrate. Each individual search act takes the form of either a probe or a dig (see Chap. V). There are a number of possible strategies which crows could adopt in deciding exactly where to make these searches.

1. The crows could detect some stimulus emanating from the

clams. This could be visual, auditory, tactile or even chemical. For example, water squirted from the siphon, the siphon itself, or an indentation left in the surface as it is withdrawn, could all be visible to a crow. Direct visual detection appears to be used by redshank (Tringa totanus) foraging for polychaete worms (Nereis sp.) (Goss-Custard 1977b,1981), while the black-billed magpie (Gymnorhina tibicen) hunts for scarab larvae by sound location (Floyd and Woodland 1981). Availability in such a situation would depend on the distance over which the crows can detect the stimuli and their sensitivity to size-related differences in stimulus strength or quality.

2. Crows may use some micro-topographical feature as a cue to the probable location of a clam. Preferences by clams for certain microhabitats, such as near a stone, and competition for these locations, could result in fine grain differences in the spatial distribution of the size classes. If crows exhibit a tendency for probing in such areas, clams preferentially occupying them will be at higher risk. Prey availability will be a function of the degree of the distributional differences and the crows' foraging preferences.
3. The siting of each search may be randomly determined. Under certain conditions the oystercatcher (Haematopus ostralegus) has been shown to use randomly directed probes to search for the bivalve Macoma balthica (Hulscher 1982). Since

northwestern crows only dig and probe in the clam bed and show a preference for areas containing a high density of clams (Chap. V), this process cannot be totally random. However, this concentration of effort is probably the result of previous experience. Having decided the approximate location in which to search, based on past success, the siting of each dig or probe may be independent of the presence of a clam. Using such a strategy, initial detection of a clam is almost certainly tactile, although when digging, visual detection would also be possible. Preliminary observations suggested this to be the most likely of the three strategies and the exact determinants of prey availability using such a strategy will be developed in the model.

A random search hypothesis gives two testable predictions. Firstly, crows may detect clams directly. This may be because of some stimulus generated by the clams or because the crows have learnt to associate the presence of a clam with some feature of beach topography. Then the probability that a search will be successful will be determined by the reliability of those clues and not prey density. Since both clam density and surface topography can be manipulated, this prediction can be tested experimentally. Secondly, if crows search at random, success per probe or dig should be directly proportional to clam density. Since the clam bed contained patches of high and low clam density, this prediction could be tested observationally.

METHODS

All observations and experiments were carried out on Mitlenatch Island, British Columbia, during the summers of 1979 to 1982. The island is described in Chap. II and by Butler (1974,1980). The data were collected from the clam bed in the subsidiary area of Camp Bay known as Well Bay (Map 2).

Search intensity and the presence of clams

To test the prediction that rates of probing and digging should be independent of the presence of clams, I established two sets of six, 1 by 1 m experimental plots. One set was located in Well Bay and the other one in the nearby Prom Bay clam bed (Map 2). Horizontal movements of clams into and out of the plots was limited by 15 cm barriers of plywood or hardware cloth sunk vertically into the beach, with their upper edges just below the surface. The location of each plot was marked, as inconspicuously as possible, with a stone at each corner. Each set consisted of two undisturbed control plots and four others to which were applied combinations of two experimental procedures: (i) removal of clams and (ii) elimination of surface features. The four experimental plot types were as follows:

1. A plot from which all clams were removed and the substrate replaced as normally as possible,
2. a second plot treated exactly the same as the first but with

the full complement of clams replaced after sampling. The surface of each of these two plots rapidly returned to normal with successive tides,

3. a plot from which all the clams were removed and the substrate replaced without any pieces of shell or stones showing on the surface. Features which birds may have used as cues to direct their searching were eliminated, after each high tide, by gently raking the surface of the plot,
4. a final plot, similar to the preceding one but with the clams replaced after sampling.

Initial clam densities were roughly the same in each of the plots. The plots were re-sampled after 1 mo to ensure that no clam migration had occurred. During that month (27th May to 27th June, 1980) the plots were observed for 1 h each day and the number of digs, probes and captures in each recorded.

Relationship between capture rate and clam density

A 3 by 3 m grid of string was laid out over the clam bed and the position of prominent stones in the grid used to construct a large scale (1:300) map (Map 3). Twenty five cm square quadrats at each intersection of the grid were used to determine the spatial distribution of clams. The maximum overall length (Fig. 1) of all clams found within 15 cm of the surface was measured with vernier calipers. The number of clams in 1 mm size classes was noted for each sample and they were then replaced to minimize the impact of sampling.

Areas of high and low clam density were identified from the sampling program (Fig. 8). I used the number of clams larger than 25 mm in each 25 by 25 cm sample plot as the measure of prey density. The crows′ searching intensity (the number of probes or digs per unit area) was not constant within the 2 areas (Figs. 2 and 3). To eliminate errors in the calculated capture frequency resulting from these differences, I weighted the clam density in each sample quadrat by a factor ranging from 0 to 5, corresponding to the search intensity catagories used in Figs. 2 and 3. Though such a weighting is slightly different for probes and digs, the calculated densities were very similar. The high density area was estimated to have 27 clams per quadrat (26.2 for probes and 27.2 for digs), while the low density area contained 11 clams per quadrat (10.0 for probes and 11.8 for digs). The difference in the mean number of clams per plot in the two areas is highly significant (Mann-Whitney U test, $P < 0.001$). I watched birds foraging in each of the areas and counted the numbers of digs, probes and captures. To avoid a bias towards successes, I only collected data from birds seen landing on the beach. Probes and digs were counted until the bird either took a clam or flew away.

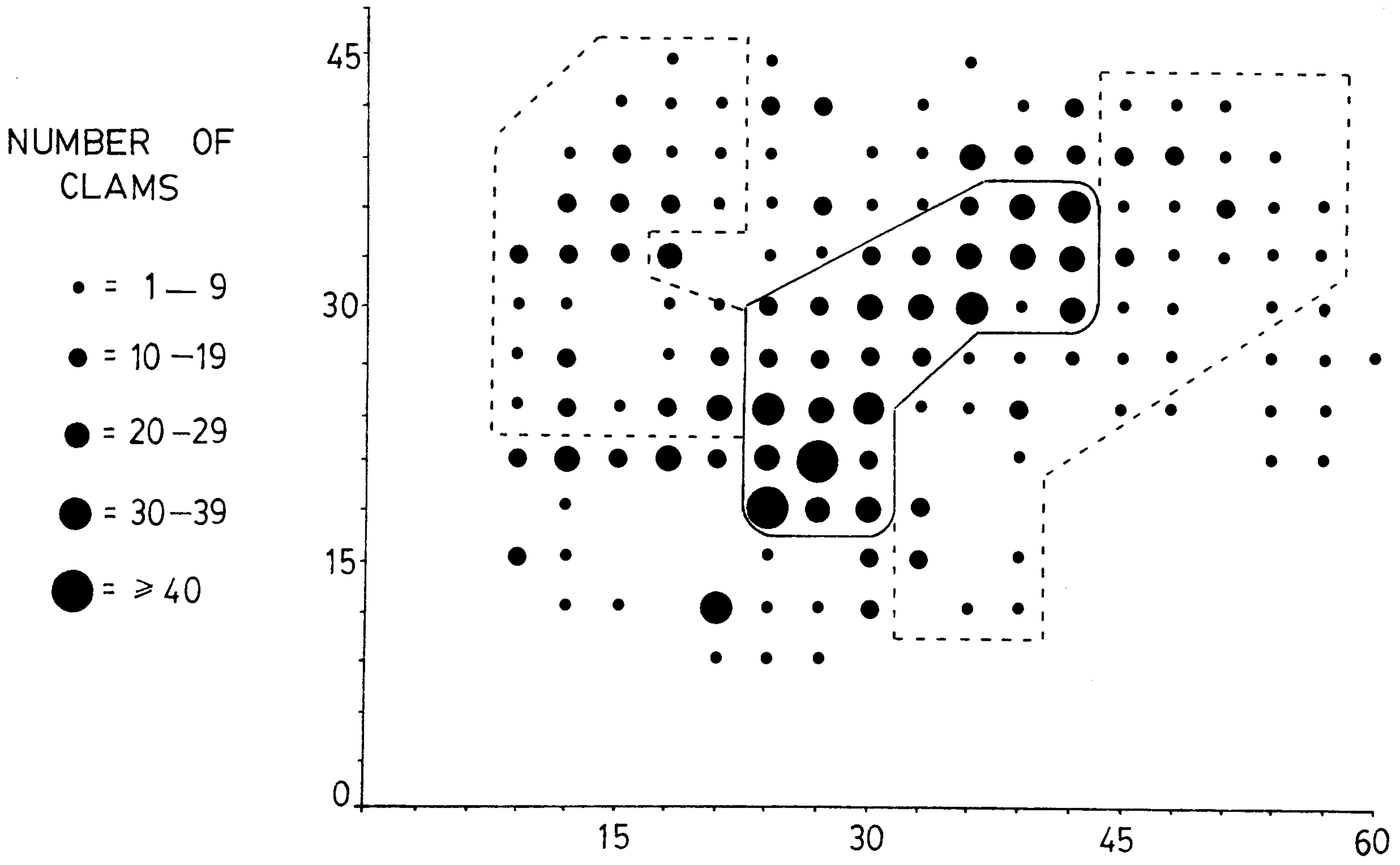


Fig. 8. Spatial distribution in Well Bay of clams larger than 25 mm. The area enclosed in the solid line is the high density area considered in the text, and those enclosed in dotted lines are the low density areas.

RESULTS

Search intensity and the presence of clams

The combined number of digs and probes recorded in each plot is shown in Table 5. The intensity of search is independent of plot type in both sets ($X^2 = 2.1$, df=5, $P > 0.75$ for Well Bay and $X^2 = 9.2$, df=5, $0.1 > P > 0.05$ for Prom Bay). This lack of dependency was also true for the pooled data from both sets ($X^2 = 2.5$, df=4, $P > 0.5$). A comparison of experimental plots containing clams (#'s 2 & 4) and those without (#'s 1 & 3) shows that the number of probes and digs per plot is independent of the presence of clams ($X^2 = 1.57$, df=1, $0.3 > P > 0.2$). Raked plots (#'s 3 & 4) were similarly shown to be searched as frequently as unraked ones (#'s 1 & 2)($X^2 = 0.37$, df=1, $P > 0.9$).

Capture rate and clam density

The proportions of successful probes and digs in areas of high and low clam density is shown in Table 6. Because the volume of substrate searched by a dig is greater than that searched by a probe the success of the two modes is considered separately. The crows were significantly more successful in areas of high prey density than in low density areas for both digs ($X^2 = 14.0$, df=1, $P < 0.001$) and probes ($X^2 = 12.5$, df=1, $P < 0.001$).

Table 5. Number of individual searches (probes plus digs) observed in different experimental plots in Well and Prom Bays. Each of the 4 plot types was treated with a combination of 2 experimental procedures; (i) removal of all clams and (ii) obliteration of surface **features** by daily raking. All experimental plots were sampled for clams prior to the observation period, while control plots were left completely undisturbed.

	Number of searches						
	Unraked		Raked				
Site	No clams	clams	No clams	clams	Controls		Total
Well Bay	14	16	12	10	15	16	83
Prom Bay	7	9	10	20	10	11	67
Totals	21	25	22	30	25	27	150

Table 6. The number of successful and unsuccessful searches made in areas of Well Bay containing high or low densities of clams. The percentage of the total number of probes or digs in each area is given in brackets.

	Number of searches			
Outcome of	Probes		Digs	
searches	High	Low	High	Low
Unsuccessful	56 (77%)	138 (93%)	61 (59%)	162 (79%)
Successful	17 (23%)	10 (7%)	42 (41%)	42 (21%)
Totals	73	148	103	204

Both results support the contention that crows usually dig and probe without reference to the location of a clam. Further evidence was sought by replacing half the clams from two 1 m^2 plots with shells stuffed with plasticene. I expected a randomly searching crow to find and take equal numbers of normal and stuffed shells. Unfortunately, clams from one plot were washed to the surface by a violent storm and insufficient numbers of clams were taken from the other plot to perform meaningful statistical analyses. However, over a 1 mo period, two normal and four stuffed clams disappeared from this plot. Random searching is also suggested by frequent observation of crows probing more than 10, and once as many as 21 times before finding a clam. These large numbers seem inconsistent with direct detection of prey. For instance, black-billed magpies achieved a success rate per probe as high as 95% using auditory detection of buried scarab larvae (Floyd and Woodland 1981).

Although I did observe birds rushing forward and pulling a clam from the beach, apparently having seen some indication of its presence, such incidents were rare. Thus, both the normal behavior of the birds and the results of these experiments suggest the random location of probes and digs.

THE MODEL

The derivation of size-specific availability indices presented here, incorporates the following assumptions.

1. Crows cannot detect littleneck clams directly and must therefore probe and dig at random.
2. Clam movements, in both horizontal and vertical planes, are negligible compared to the search speed of the crows.
3. Clams are considered simplistically as a 2 dimensional object lying in and of the same dimensions as the plane of their greatest horizontal cross-sectional area. This will be referred to as the plan area (Fig. 1), and represents the maximum area of each clam exposed to probes directed perpendicular to the beach surface. This is equivalent to the effective touch area defined by Hulscher (1982).
4. There is no vertical overlap in the plan areas of clams.
5. The tactile sense of a crow is sufficiently sensitive that clams of all sizes can be detected whenever touched.

Under these restrictions, the major factors considered to contribute to size-dependent differences in availability are (i) the plan area of clams, (ii) the frequency distribution of search depths and (iii) the vertical distribution of different size classes of clams in the beach. The plan area and search depth distribution define a three dimensional space that is searched for each size class of clam by the average probe or dig. The efficiency of this search is then dependent on the distribution of that size of clam within the prescribed search space. This product of the physical space searched and the probability of a clam being located in that space will be referred to as the effective search volume.

Availability indices are then based on a comparison of the effective search volumes for each size clam. Because they describe different shaped search volumes, indices for probing and digging will be derived separately. Definitions of each of the variables used in calculating relative availabilities are given in Table 7.

Availability of clams to probing

Consider the simple situation of a predator probing for a circular 'prey' lying in a plane perpendicular to the direction of the probe. Any prey whose centre is less than its own radius from a probe will be detected. Even though the plan area of a clam is not circular, the above relationship will hold if the clams' orientation is random relative to probes. Although they typically lie with their anterio-dorsal margin perpendicular to the beach surface (Fig. 1), the clams' orientation about this vertical axis is apparently random. The extreme conditions would be with either the long or short axis of the plan area in radial alignment with the probe. The former would result in the maximum radius of detection and the latter, the minimum. Approximation of the plan area to a circle of equal area will average these differences.

Table 7. List of the symbols used in the text for the determination of the relative availability of clams of different size classes.

C_{ij} = proportion of clams of size i in depth interval j
EV_{ij} = effective search volume in depth interval j for a clam of size i
EV_i = effective search volume at all depths for a clam of size i
V_{ijy} = actual volume searched for a clam of size i, in depth interval j, by a hole dug to maximum depth y
V_{ij} = actual volume searched for a clam of size i, in depth interval j, by all digs or by an average probe
V_i = actual volume searched for a clam of size i in each depth interval through which a probe passes
Q_j = proportion of probes penetrating to depth interval j or deeper
Q_y = proportion of holes dug to maximum depth y

r_i = average radius of the greatest horizontal cross-sectional area of a clam of size i
r_p = average radius of the crows' bill at mid-length
r_{jy} = radius in depth interval j of a hole dug to maximum depth y
R_i = total radius searched for a clam of size i in each depth interval

RAP_i = relative availability of a clam of size i to probes
RAD_i = relative availability of a clam of size i to digs
RA_i = relative availability of a clam of size i to all searches

Table 7 continued:

d = proportion of all searches which are digs

p = proportion of all searches which are probes

n = vertical dimension of the depth intervals

Let V_i be the volume searched for a clam of the ith size class in any particular depth interval. For a probe, this will be roughly constant at each depth through which the probe passes. It will be a cylinder of height n, the dimension of the depth interval, and with a base radius (R_i) equal to the radius of the probe (r_p) plus that of the clam (r_i):

$$R_i = r_i + r_p \tag{1}$$

Then

$$V_i = \pi . n . (R_i)^2 \tag{2}$$

The average volume searched by a probe for the ith class clam in a single depth interval, j, is denoted by V_{ij}. This will be the product of the volume searched for that size clam and the proportion of probes penetrating to depth j or deeper (Q_j):

$$V_{ij} = \pi . n . Q_j (r_i + r_p)^2 \tag{3}$$

The effective volume searched (EV_{ij}) is the product of the physical space searched and the probability of a clam of size i being located in that
space (C_{ij}).

$$EV_{ij} = C_{ij} . V_{ij} \tag{4}$$

Then the total effective volume searched at all depths (EV_i) is the sum over j of all EV_{ij}.

$$EV_i = \sum^{j} EV_{ij} \tag{5}$$

The derivation of the effective search volume is shown schematically in Fig. 9. The relative availability of any particular size class (RAP_i) is then expressed as the proportion that EV constitutes of the sum of the effective search volumes for all sizes.

$$RAP_i = \frac{EV_i}{\sum^{i} EV_i} \qquad (6)$$

where RAP_i is the relative availability index of the ith size class to probing.

Availability of clams to digging

Unlike the situation with probes, the volume searched in any depth interval by digging is a function of the overall depth of the hole dug. The volume searched just beneath the surface will be much larger for a dig which penetrates to a depth of 5 cm than for one which only reaches 1 cm. For a dig to a maximum depth y, the radius of the hole in the j th depth interval (r_{jy}) will be given by some function of y. The dimensions of a dig hole used here are shown schematically in Fig. 10.

V_{ijy}, the volume searched for the ith class of clams in the jth depth interval by a dig to a maximum depth y, is given by

$$V_{ijy} = \pi . n . (r_{jy} + r_i)^2 \qquad (7)$$

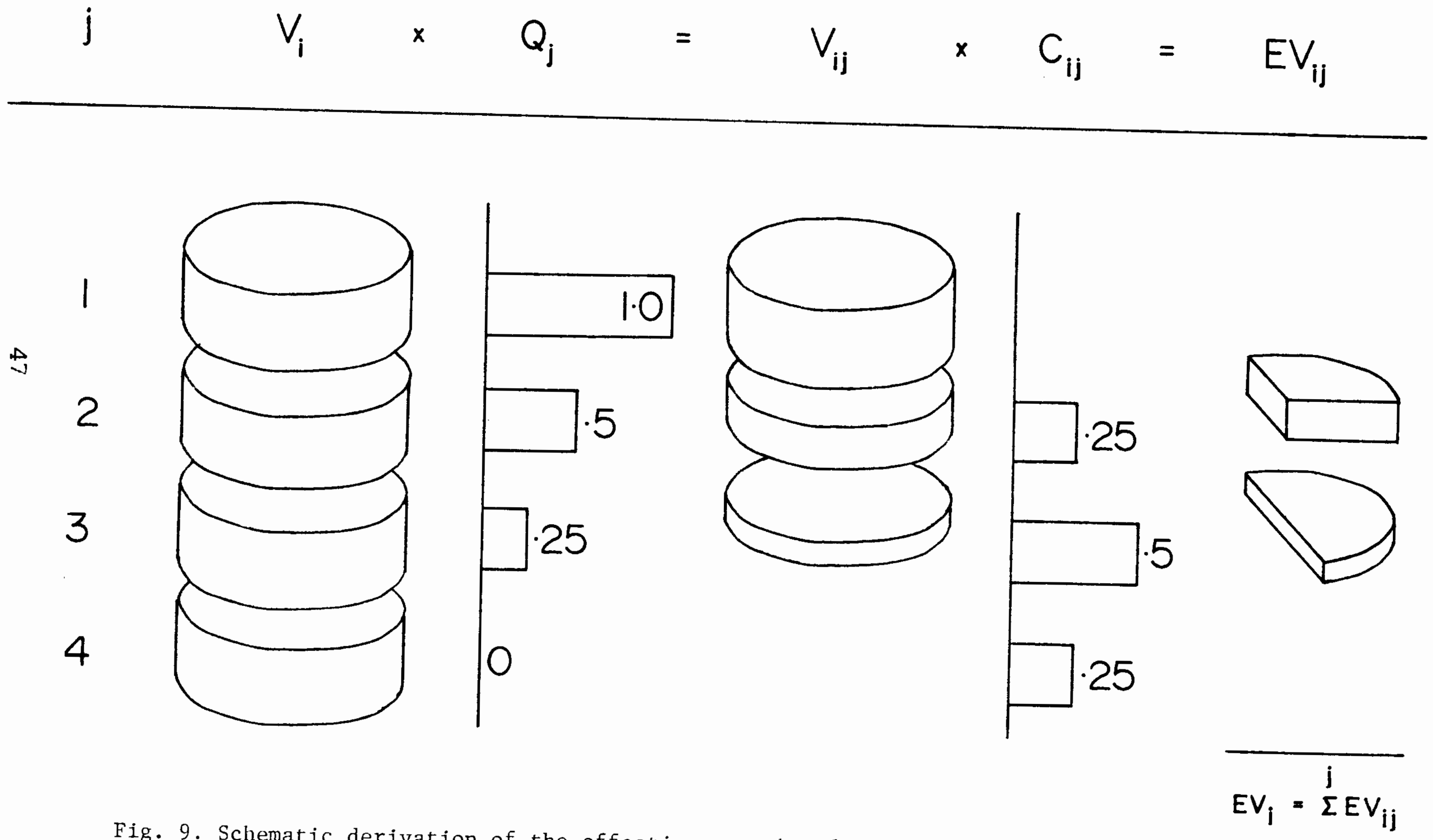


Fig. 9. Schematic derivation of the effective search volume of a probe for a clam of size i.

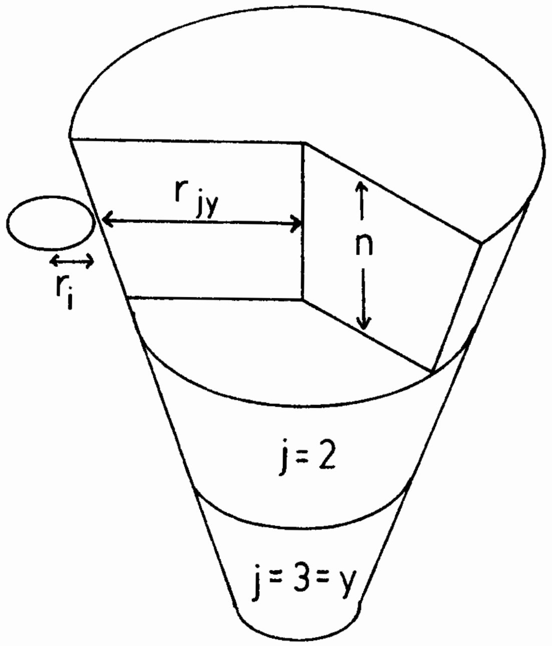


Fig. 10. The dimensions of a dig hole used in calculating effective search volumes.

If Q_y is the proportion of digs to depth y, then the average volume searched by all digs, within the jth depth interval, for clam size i (V_{ij}) is

$$V_{ij} = \pi . n . Q_y . (r_{jy} + r_i)^2 \qquad (8)$$

Then following the same line of reasoning used to develop the availability indices for probing (Equations 4 to 6), the availability index of the ith size class for digging (RAD_i) will be

$$EV_{ij} = V_{ij} . C_{ij} \qquad (9)$$

$$EV_i = \sum^{j} V_{ij} . C_{ij} \qquad (10)$$

$$RAD_i = \frac{EV_i}{\sum^{i} EV_i} \qquad (11)$$

The derivation of RAD is shown schematically in Fig. 11.

An overall availability index to both digging and probing (RA_i) is obtained by summing the products of the separate indices and the proportions that digs or probes comprise of the total search effort. Thus

$$RA_i = p . RAP_i + d . RAD_i \qquad (12)$$

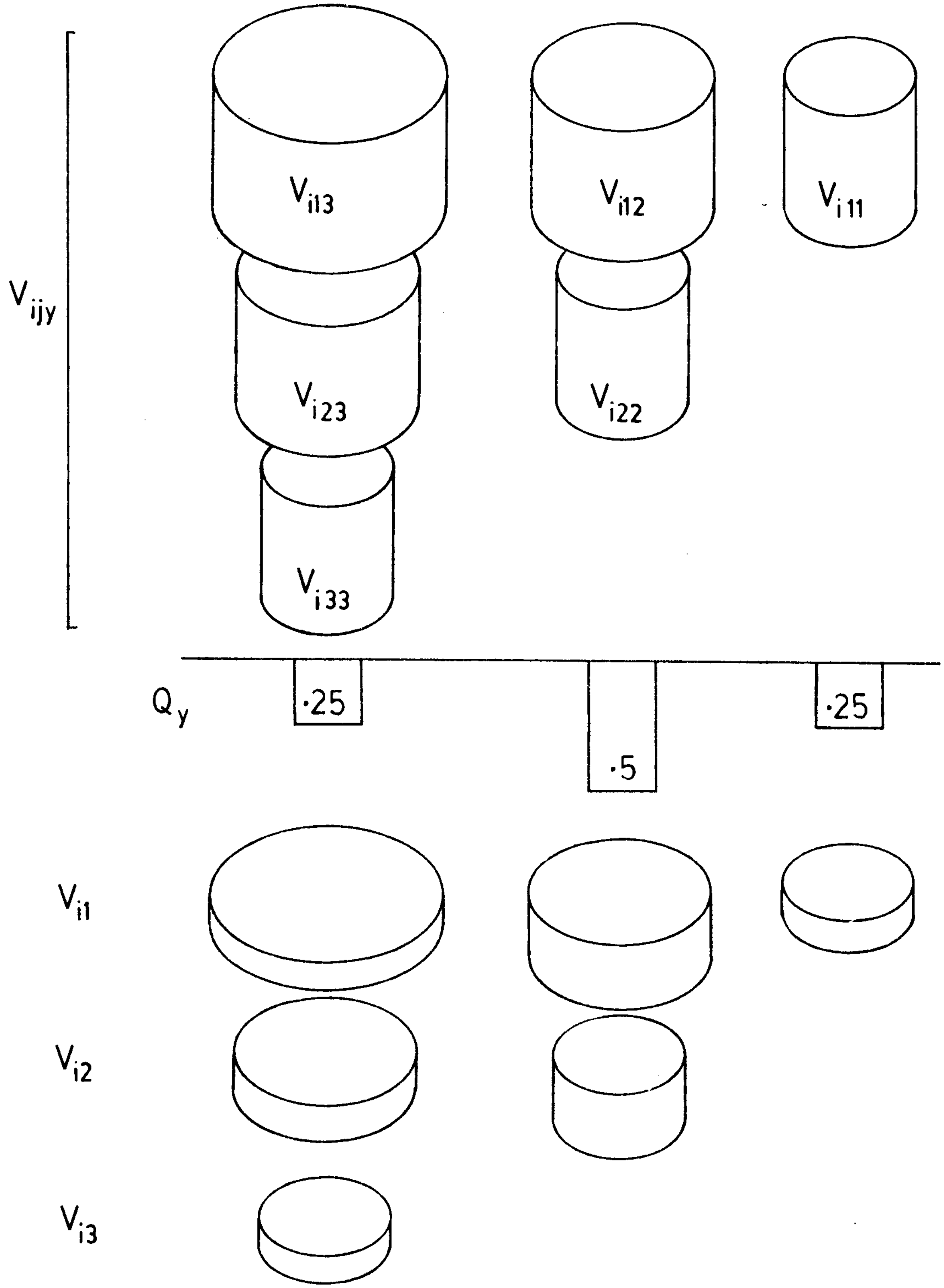


Fig. 11. Schematic derivation of the average volume searched for a clam of size i in each depth interval by all holes.

where d and p are the relative proportions of digs and probes, respectively.

PARAMETERS OF CROW FORAGING TECHNIQUES

The model incorporates five factors related to the physical and behavioral properties of crows:

1. the bill (probe) dimensions,
2. the depth distribution of probes,
3. the depth distribution of digs,
4. the ratio of digs to probes, and
5. the shape of digs.

METHODS

Bill dimensions were measured from 11 museum specimens. Length was measured from the base of the prominent tuft of nasal feathers to the tip of the bill. Depth and width were measured at mid-length. The proportion of the length of the bill inserted into the beach was then used to gauge the maximum depth of each dig and probe. The distal ends of the nasal tufts, which extend to approximately mid-length, provided a useful subdivision of the bill for these estimates. I estimated the depth of each search to fall into 1 of 5 categories: 1/4, 1/2, 3/4, 1 and >1 bill lengths. The depth distributions and the ratio of digs to probes were determined from direct observation of birds foraging on the beach. It is important to distinguish between the volume searched by the birds and the volume actually excavated in removing a clam from the beach. When a crow had located a clam, it often had to enlarge the hole considerably before the clam could be extracted. Only unsuccessful searches were used in determining the depth distribution of probes and digs.

Plaster casts were made of recently dug holes. Once again, as far as possible, only holes dug during unsuccessful searches were used. The diameter of each cast was measured at the surface and at 1 cm intervals below it. Because of the irregular shape of most of the casts, the mean of the greatest and smallest diameters was used as an approximation of the average diameter at that depth.

The mean values of all parameters presented in this and all subsequent chapters are given ± 1SE unless otherwise stated.

RESULTS

Bill dimensions

The average length of the bill was 4.4 ± 0.01 cm. This lies within the range of 4.1 to 4.8 cm given by Gabrielson and Jewett (1970). The mean depth and width at mid-length were 1.5 ± 0.04 and 1.0 ± 0.03 cm, respectively. Crows usually probe with their bill slightly open so that the upper and lower margins are roughly parallel. Held this way the bill is approximately cylindrical with a mean radius of 0.65 cm.

The depth distribution of probes

The depth distribution of 353 probes, which constituted 55% of the observed search acts, is shown in Fig. 12. A regression of the number of probes on the mid-interval depth in cm gave the following relationship.

$$\# \text{ probes} = 159.9 - 32.5(\text{depth}) \quad (R=-.99,\ n=5)$$

Since the availability model was based on discrete depth intervals of 0.5 cm, rather than units of bill length, the above regression was used to calculate the number and proportion of probes expected in the smaller intervals. The resulting distribution of probe depths, used in the calculation of availability, is also shown in Fig. 12.

The depth distribution of digs

Because the difficulty of penetrating the substrate with a single thrust increases with depth, the crows resorted to digging to reach depths which would otherwise have been inaccessible. The frequency distribution of the maximum depths of 289 digs is shown in Fig. 13. The mean depth of digs was 2.5 cm with a standard deviation of 0.94 cm, compared to 1.6 ± 0.8 cm for probes. Calculation of the availability indices was done assuming the distribution of dig depths to have been normal with a mean and standard deviation as measured. The expected frequency distribution of digs within each depth interval, calculated under this assumption, is also shown in Fig. 13. The observed and predicted distributions do not differ significantly

($X^2 = 5.97$, $df = 2$, $0.1 > P > 0.05$).

The shape of digs

The average radius of digs at 1 cm intervals from the surface, in holes of different maximum depth, is shown in Table 8. A regression of radius (r) on both depth interval (j) and maximum hole depth(y),

$$r = 1.22 - 0.089(y) + 0.435(j) \quad R = 0.96$$

was fitted to the data. The digs are probably not simple inverted cones because at greater depths a crow cannot just rotate its head to move sand to the side but must lift it also.

PARAMETERS OF THE CLAM POPULATION

The three factors which are thought to influence the clams' vulnerability to crow predation are their plan area, mobility within the substrate and depth beneath the beach surface.

METHODS

Plan area

The plan area was defined as the greatest horizontal cross sectional area of a clam, in its normal orientation in the beach. Orientation is most commonly with the margin of the shell from the umbo to the anterior end (the lunule) perpendicular to the surface and the posterior or siphon end uppermost (Fig. 1). The plan area was assumed to be the same as the area of

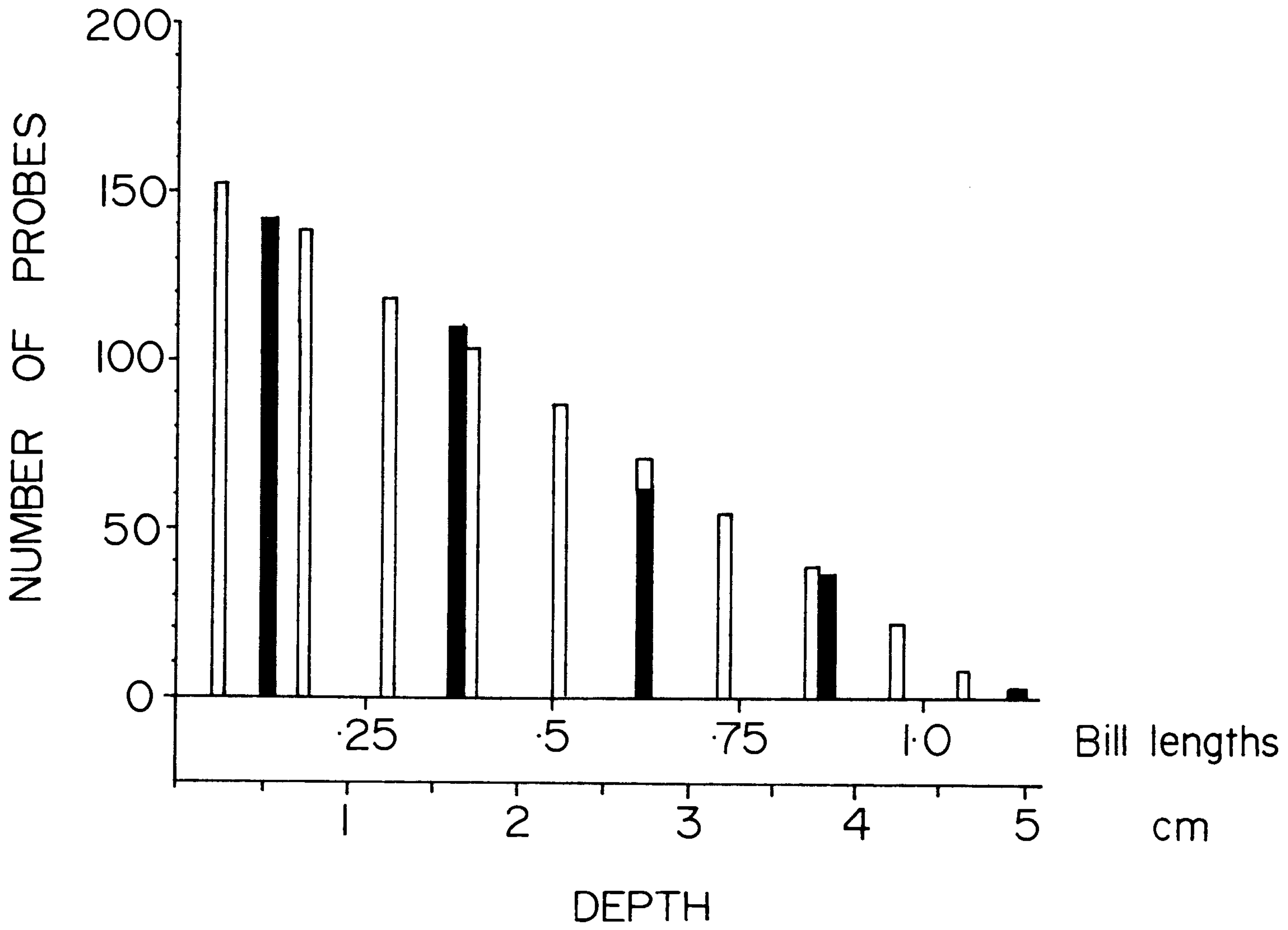


Fig. 12. Depth-frequency distribution of 353 probes (solid bars). The linear regression: # probes = 159.9 - 32.5(depth in cm) was fitted to the data and used to calculate the proportion of probes in 5 mm depth intervals (open bars).

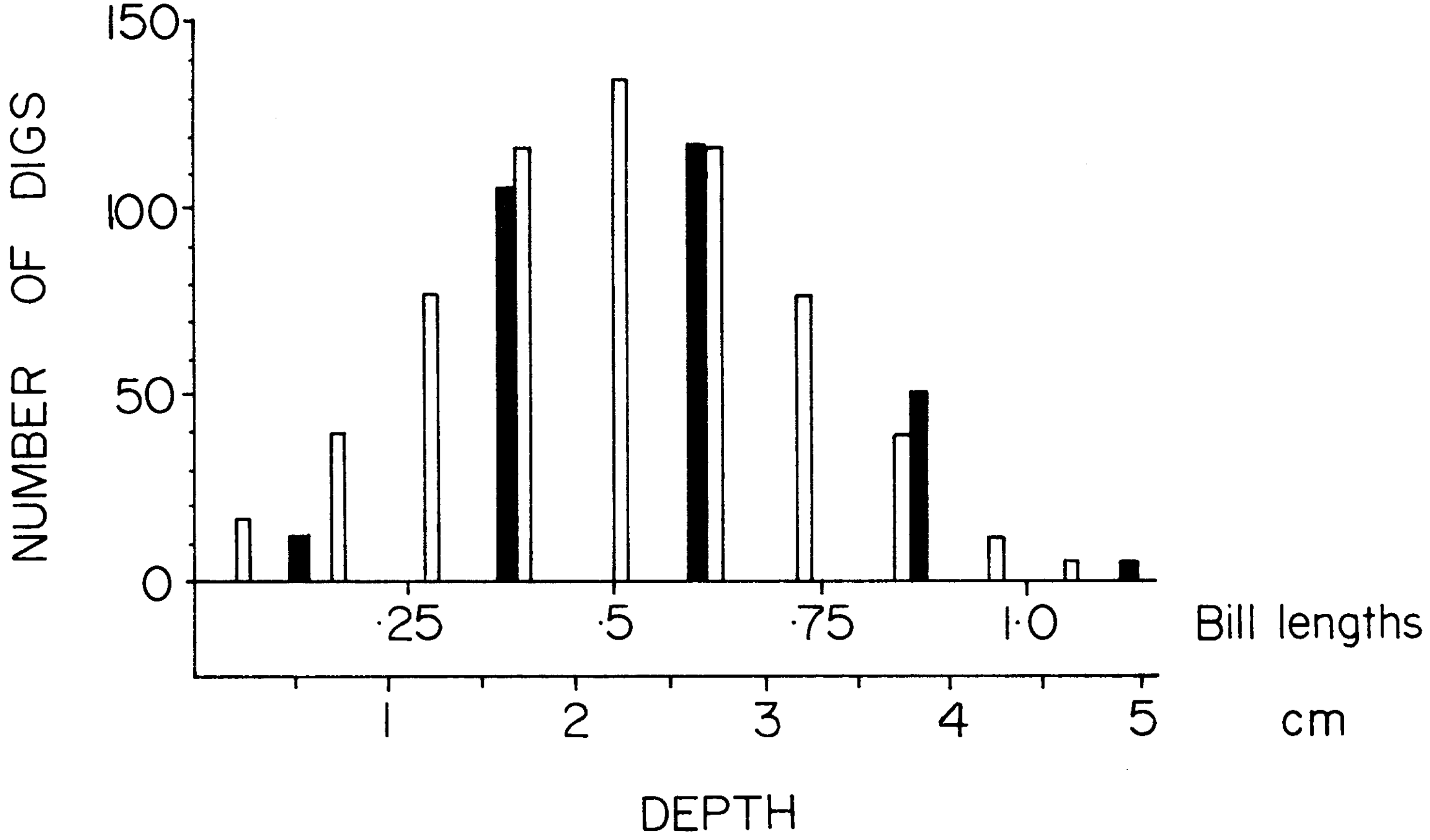


Fig. 13. Depth-frequency distribution of 289 digs (solid bars). In the calculation of availability indices it was assumed that this distribution was normal. The open bars show the proportion of digs in each depth interval under this assumption.

Table 8. Mean radius (mm) of holes, dug by northwestern crows to different depths, measured at 1 cm intervals from the beach surface.

Depth interval (cm)		Maximum depth of hole (cm)				
		0-1	1-2	2-3	3-4	4-5
	n=	3	14	11	20	9
0-1		1.7	2.2	2.3	2.8	3.0
1-2			1.5	1.7	2.3	2.3
2-3				1.3	1.7	1.9
3-4					1.1	1.6
4-5						1.2

cross-section through the umbo and at right angles to the hinge (Fig. 1). The outline of this cross-section, of different size clams, was found using a carpenter's contour gauge. The maximum height of the shell, perpendicular to the plane of the plan area, was also measured for use in the calculation of the depth distribution of the clams. The cross sectional outlines were traced onto bond quality paper of known weight per unit area. The tracings were cut out, weighed and their areas calculated.

Vertical migration

Vertical movements of clams were observed in a 50 by 7 by 30 cm plexiglass container. This container was housed in a wooden sleeve sunk into the clam bed. Fitted handles allowed it to be lifted from the sleeve for observation. At the start of the experiment the container was filled with material from the beach into which were placed a number of individually marked clams. The container was then lowered into the sleeve and left undisturbed for a 7 d recovery period. It was then withdrawn from the sleeve at 2 h intervals throughout the low tide period for 7 consecutive days. The position of any clam visible through the plexiglass was marked with a grease pencil.

The reaction of clams to disturbance of the surface was also investigated by direct observation. Clams were placed into the container which was left on the beach for an adjustment period. Following this, the tip of a pencil was thrust into the sand to touch any visible clams and their reactions noted.

Depth distribution

The depth of clams below the beach surface was measured from a leveled, 25 by 25 cm angle iron frame mounted on short (5 cm) legs. The gradient of the beach was so slight compared to the size of the quadrat that it was ignored. A horizontal bar was placed across the top of the frame and the distance from the bar to the beach measured at twelve points in each quadrat. The average of these points provided a datum plane for the measurement of clam depth. The clams were gently exposed using a kitchen fork and paint brush. The distance from their uppermost tip to the bar was measured with a steel ruler. The availability model was based on the depth of greatest cross sectional area of a clam.

RESULTS

Plan area

Plan area increased as a power function of maximum shell length,

$$\text{Plan area} = 0.173\ \text{Clam length}^{2.19} \qquad (n=50,\ R=.99)$$

and clam radius (r_i) simply by

$$r = (\text{clam area}\ /_{\pi})^{5}$$

Vertical movements

Although clams moved into and out of view, detectable changes in position only occurred over a period of days. The typical reaction to disturbance was shell closure rather than trying to bury deeper. Similar slow rates of movement were observed by Pearson *et al.* (1981). In their experiments it took over 2 h for 50% of clams (*Protothaca staminea*), 26 to 35 mm in size to bury themselves. Such rates are obviously of little consequence in the present study.

Depth distribution

Regressions of depth on clam size for 7 sample plots (Table 9), indicate considerable variation in this relationship at different points on the beach. However, an analysis of covariance showed no significant heterogeneity between the samples in either slope ($F = 0.16$, df = 6,37, $P > 0.5$) or elevation ($F = 1.71$, df = 6,37, $P > 0.05$). The 7 samples were consequently pooled and the resulting depth frequency distribution is shown in Fig. 14. An analysis of variance of the pooled data showed a significant difference between the depth distribution of the size classes ($F = 22.5$, df = 5,242, $P < 0.001$), but this difference could not be described by a simple linear relationship ($F = .71$, df = 1,4, $P > 0.2$). In lieu of any simple, biologically meaningful relationship between depth and clam size, the depth distributions used in calculating the availability indices were assumed to be normal, with means and

Table 9. Relationship between clam length (x) and its depth below the beach surface (y) in mm.

Sample #	n	Regression equation
1	44	$y = 0.28x + 16.5$
2	20	$y = 0.19x + 10.9$
3	42	$y = 0.68x - 0.8$
4	55	$y = 0.06x + 8.7$
5	36	$y = 0.19x + 9.0$
6	35	$y = 0.29x + 6.2$
7	16	$y = 0.32x + 6.4$

variances equal to those of the pooled data (Fig. 14). To these values were added the height between the tip of the shell and the maximum plan area, since depth measurements were made from the beach surface to the tip of the shell, while the model was based on the depth of the greatest plan area. This height is given by

Height = 0.22 Clam size + 3.2 mm. (n=50, R=.99)

PREDICTIONS AND TESTS OF THE MODEL

Availability to probes

The calculated relative availability of different size clams to probing was an increasing function of length (Fig. 15). In Well Bay the clams were close to the surface, relative to the depth of crow probes, and with only a weak relationship between burying depth and clam size. Consequently, the strongest influence on the relative availability of different size clams was their plan area. Increasing the dependency of burying depth on clam size tended to reverse this relationship, as fewer of the large clams were within reach of the probing birds.

Availability to digging

The availability of clams to digging crows was inversely proportional to clam size (Fig.15). Because the holes were consistently wider at the top than at the bottom, this

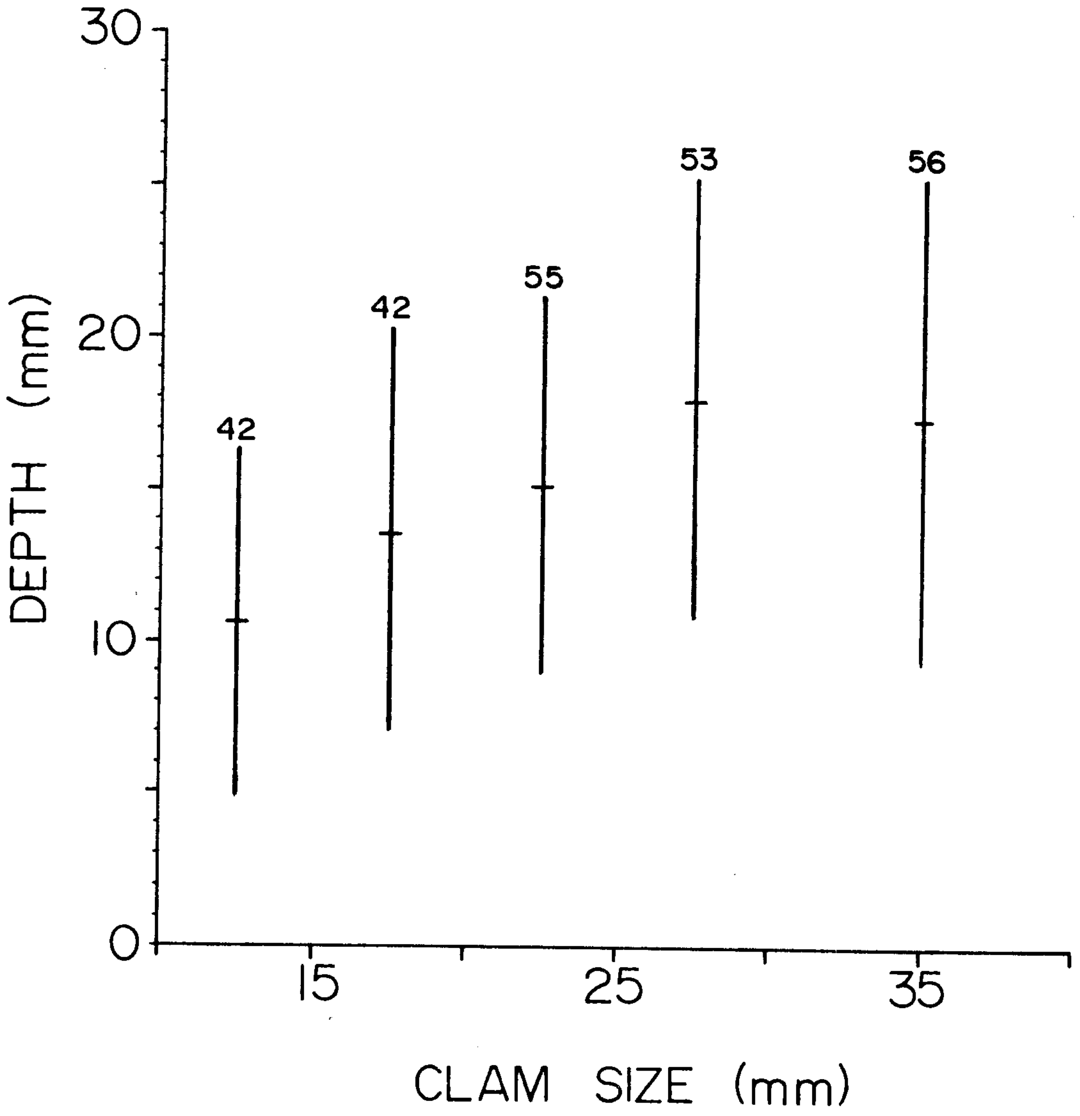


Fig. 14. Mean depth (± 1 SD.) of different sized clams from the pooled data of 7 sample quadrats in Well Bay.

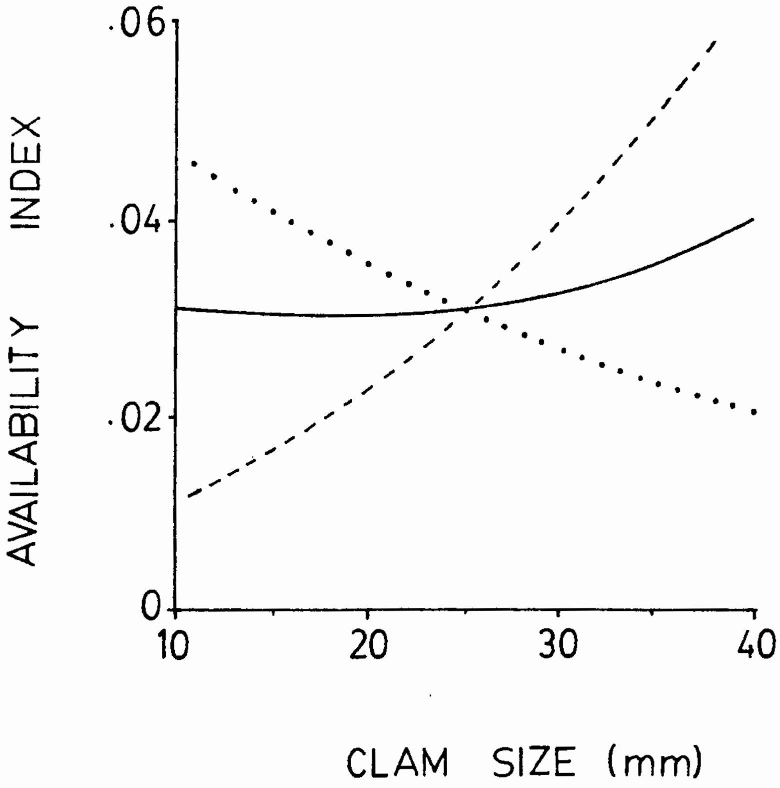


Fig. 15. Availability indices of different sized clams to probing (----), to digging (....) and to probing (55%) and digging (45%) combined (——).

relationship is qualitatively similar for most realistic changes in the depth distribution of both digs and probes.

The overall availability of different size clams, from the weighted combination of the individual availabilities to digs and probes (Equation 12), is also shown in Fig. 15.

Because of the suspected preference of crows for larger clams, it was difficult to validate the performance of the model by comparing its predictions with the performance of the birds. However, two possible tests presented themselves. Firstly, simulation of the process of probing was straightforward and was used to produce a size distribution of clams encountered by probing without the confounding influence of preference. Secondly, the calculation of availability indices was based on the volume searched at different depths for clams of different sizes. By making some simplifying assumptions it was possible to estimate the probable success rate per dig or probe from areas of known prey density.

Probe simulation

The two distal segments of my index finger have roughly the same dimensions as a crow's bill: a 5 cm cylinder with a radius of 0.75 cm. I made 1500 probes, to the depth of the second knuckle, with my index finger, in a selected 10 by 10 m area of the beach. This was located in an area of high clam density and with its centre at coordinates 39,33 on Map 3. The size distribution of live clams in this area was known from the sampling program and was modified, according to the predictions of relative availability from the model, to reflect this search method. Fig. 16 shows the size distribution of 524 clams located by my finger probes with the adjusted distribution of 369 clams from the sample quadrats. Although the fit is not exact, there is at least a qualitative agreement between the two distributions.

Success rate per dig and probe

In the first section of this chapter, areas of high and low density of clams larger than 25 mm were identified (Fig. 8), and the success rate of both digs and probes in the two areas established (Table 6). If the model of availability generated realistic effective search volumes, it should be possible to predict how successful the crows are while searching in these areas. To simplify the problem, I calculated the probability of a crow locating an average clam by a probe or dig of average dimensions. A clam of 32 mm is both the average size eaten by the crows (Chap. VII) and approximately the size with the mean plan area for all clams larger than 25 mm found in the beach. The average depth of a 32 mm clam was measured to be 28 mm. At this depth the cross sectional area of the effective search volume of an average probe is 4.8 cm^2 , while that for the average dig is 11.3 cm^2. From the mean number of clams per 25 by 25 cm quadrat in the high and low density areas, I calculated the mean number of clams per probe or dig cross-sectional area.

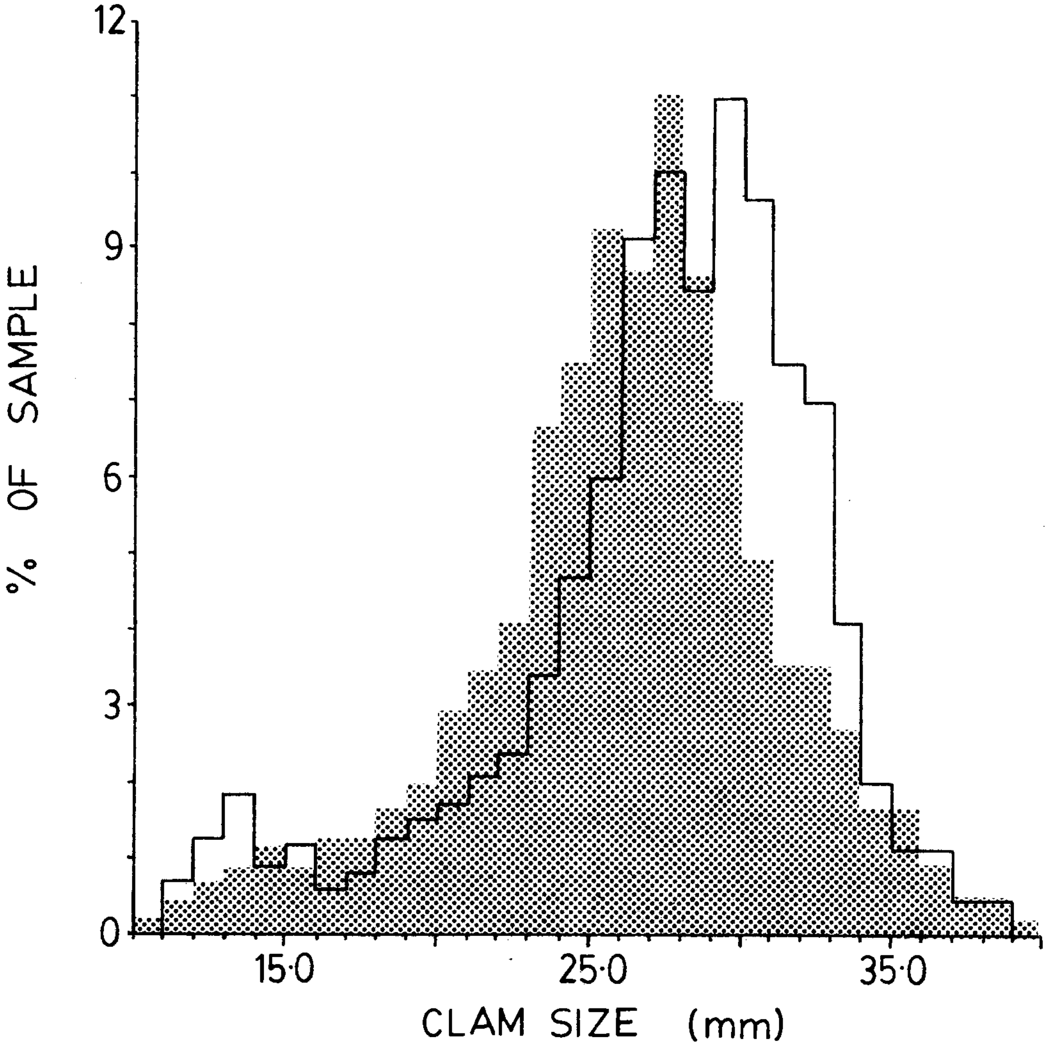


Fig. 16. Size-frequency distribution of 524 clams found by finger probes (....) and the distribution of 369 clams from beach samples in the same area, adjusted to reflect size related differences in availability to finger probing (——).

The probability of there being no clams in such an area (i.e. that the probe or dig would be unsuccessful) was then calculated from the proportions of a Poisson distribution, with a mean equal to the number of clams per probe or dig cross-sectional area. The probability of a dig or probe not locating a clam predicted by these calculations agrees closely with the observed success rate (Table 10).

A posteriori support for the model comes from comparing Ivlev′s (1961) electivity indices for each of the size classes of clams which were presumed always to be taken if encountered by crows on Mitlenatch. For the preferred classes, the relationship between the number of clams in each class should be the same as the relationship between the numbers of each class eaten by the crows. For example, consider a simple system of five size classes containing 24,12,6,4 and 2 detectable clams. If the class containing 24 clams is ignored by the predator, the relative proportion of prey taken from the four remaining classes, asssuming 100% preference, should be 6:3:2:1. The values of Ivlev′s electivity index for each of these groups should be equal. The electivity indices for the whole size range of clams is shown in Fig. 17. For those size classes which are invariably taken (those over 31 mm), there is no trend for the values of the electivty indices to either increase or decrease. Although there is some deviation from uniformity, this is mainly in classes containing less than 0.5% of either the clams available or eaten. There is no significant non-zero relationship between electivity indices and size. Such a relationship is only consistent with the crows taking clams from these size classes in the same proportions as their predicted availabilities.

While the rigor of the above tests of the model's validity is reduced by the number of simplifying assumptions, the results do suggest that the model performs in a way which is consistent with the crows' foraging methods.

Table 10. The number of successful and unsuccessful probes and digs observed in areas of Well Bay containing high or low densities of clams, compared with the number predicted by the availability model.

	Unsuccessful		Successful	
	Observed	Predicted	Observed	Predicted
High clam density:				
Probes	56	59.1	17	13.9
Digs	61	62.8	42	40.2
Low clam density:				
Probes	138	136.2	10	11.8
Digs	162	167.3	42	36.7

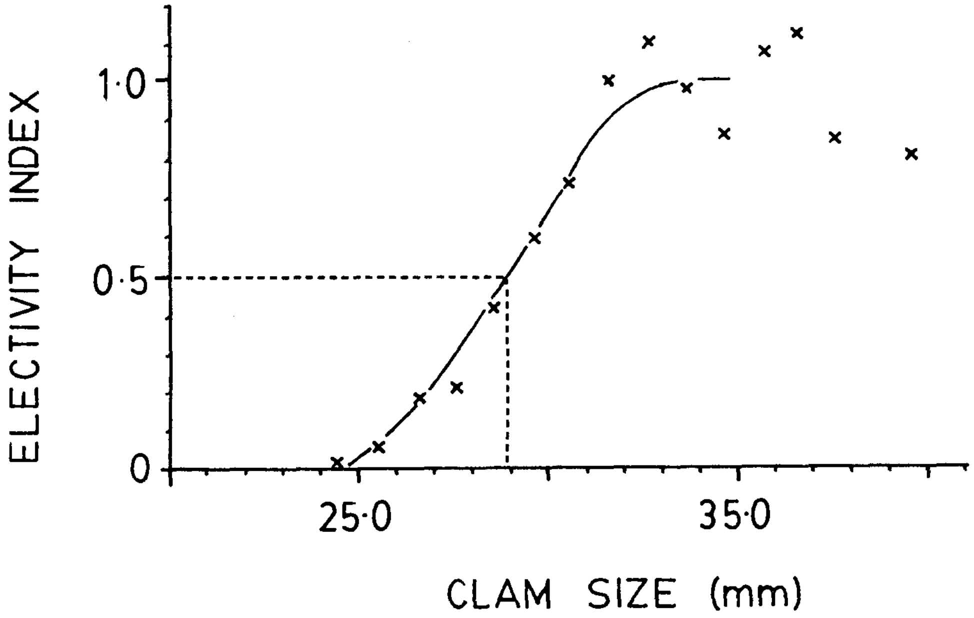


Fig. 17. Normalized electivity indices, calculated as the proportion of each size class in the diet compared to its adjusted proportion in the environment, for each size class of clam. Indices are normalized to the mean of the indices of all size classes greater than 31 mm.

VII. DIET SELECTION BY ADULT CROWS

INTRODUCTION

Most current models of diet choice (Charnov 1976, Krebs *et al*. 1977) assume that predators can assess the potential rate of net energy gain from consuming different prey types, and rank them accordingly. If prey types are added to the diet in order of decreasing energetic profitability, each addition will reduce the time and energy spent searching for acceptable prey. However, it will also decrease the average rate of energy gain per capture. The maximum rate at which energy can be extracted from the possible range of prey types will result when, for any further increase in diet breadth, the reduction in energy per capture is greater than that saved by the shortened search time (MacArthur and Pianka 1966, Schoener 1971, Pyke *et al*. 1977, Krebs 1978). Because of the profusion of data required (gross energy value of prey, energetics of the foraging process and prey densities) few field studies of predation have attempted to identify this maximum (Werner and Mittelbach 1981).

The purpose of this chapter is twofold:

1. To calculate the potential energy gain, from a variety of diet breadths, for a predator foraging naturally on a wide size range of a single prey species. The predicted optimal

diet is then compared with that taken by the predator.

2. To test the ability of this predator to assess and rank the net value of different sizes of that prey species. Ebersole and Wilson (1980) have shown that mice (*Peromyscus leucopus*) will adjust their choice of diet to reflect changes in the net value of their prey. By artificially completing part of the foraging process, the net energy gain from normally low quality types could be raised to that of a preferred type. My aim is to examine quantitatively the relationship between the energy saving and any induced changes in the predator's diet resulting from such manipulations.

Japanese littleneck clams (*Venerupis japonica*) are an important part of the diet of northwestern crows (*Corvus caurinus*) nesting on Mitlenatch Island, British Columbia (Butler 1974,1980). For several reasons, this is an excellent system in which to investigate diet selection. Firstly, this species of clam is practically immotile (Quayle and Bourne 1972 and Chapter VI) and therefore easy to sample. Secondly, the clams exist in a range of sizes which offer net rewards to a crow covering two orders of magnitude. Thirdly, shore crabs (*Hemigrapsus nudus* and *H. oregonensis*) are the only other potential prey found in the littleneck clam beds. Crows rarely fed on these and used a distinctive technique when doing so. Lastly, shells left in the restricted drop areas to which the crows typically carry clams to drop and open them (Zach 1978), provide concrete evidence of the size range of clams eaten.

THE MODEL

The model presented here is similar to that of Pastorok (1981) and differs from most others in considering the average net energy gain from a single search and capture effort rather than the expected return from a fixed period of search (see Pyke et al. 1977 for review). The advantage of the gain per catch model is that only the relative rate at which each prey type is encountered need be calculated. A list of definitions and symbols for each of the variables used in the calculations is given in Table 11.

The net energy gain from an item of the ith prey size class(E_i), after assimilation and handling costs, is given by

$$E_i = a.EG_i - EH_i \tag{13}$$

where a is the assimilation efficiency of the predator, EG is the gross energy content of an item of class i and EH the energetic cost of handling that item. Predators should rank prey by the rate at which this energy can be extracted. That is, starting with the most profitable, $E_1/TH_1 > E_2/TH_2 > E_3/TH_3 \ldots\ldots > E_n/TH_n$, where TH_i is the handling time for the ith prey class.

Table 11. List of the symbols used in the text in the determination of the optimal diet for a northwestern crow feeding on littleneck clams of different size classes.

All items subscripted i relate to clams of the i th size class.

E_i = net energy yield per clam

EG_i = gross energy content per clam

EH_i = energetic cost of handling per clam

ES = energetic cost of searching per unit time

E'_i = net energy yield per clam with its shell broken

TH_i = handling time per clam

TH'_i = handling time per clam when the shell is broken

N_i = number of clams encoutered in sampling

RA_i = relative availability

a = assimilation efficiency (assumed to be constant)

$\bar{E}_j$ = the average net energy gain per capture when the diet contains size classes 1 to j

$\bar{T}_j$ = the average intercapture time when the diet contains size classes 1 to j

TSj = the average search time per item when the diet contains size classes 1 to j

P_{ij} = the proportion of size class i in the diet when the diet contains size classes 1 to j

Let P_{ij} be the proportion that class i constitutes of all acceptable prey in a diet including classes 1 to j. The average net energy gain per prey from such a diet ($\bar{E}_j$) will be the sum of the products of net energy gain per item from each size class and the proportion of that size class in the diet, less the energy expended searching for a single item:

$$\bar{E}_j = \sum^{j} P_{ij} \cdot E_i - ES \cdot TS_j \qquad (14)$$

where ES is the unit cost of searching and TS_j the average time to search for a single prey when the diet includes size classes 1 to j. In most field studies there is a problem in relating the measured prey density to that which is probably perceived by the predator (Werner and Hall 1974, Myers _et al_. 1980, Pastorok 1981). P_{ij} cannot be calculated simply from the number of each size encountered using standard sampling techniques (N_i). This number must be modified by an appropriate scalar (RA_i) to reflect the size specific availability to the predator. Thus

$$P_{ij} = \frac{N_i \cdot RA_i}{\sum^{j} N_i \cdot RA_i} \qquad (15)$$

In the absence of other prey populations with similar size frequency distributions, but different overall densities, only one value of TS can be measured directly. If the observed diet contains classes 1 to x, and the measured average search time is TS_x, the predicted search time for any other diet range can be calculated from

$$TS_j = TS_x \cdot \frac{\sum^{x} RA_i \cdot N_i}{\sum^{j} RA_i \cdot N_i} \qquad (16)$$

The average time spent searching for and consuming a single prey item when the diet contains size classes 1 to j ($\bar{T}_j$), can be derived in a similar manner to the average energy gain. It is given by summing the products of the proportion of each size in the diet and their specific handling times (TH_i), plus the average search time.

$$T_j = \sum^{j} P_{ij} \cdot TH_j + TS_j \qquad (17)$$

The expected energy gain per unit time, for any diet width, can then be calculated from $\bar{E}_j / \bar{T}_j$ for all values of j. The optimal diet will be that producing the highest rate of energy gain.

Once the base line for diet selection has been established it should be possible to make quantitative predictions about changes in diet resulting from manipulations of prey profitability. If search time and its associated energetic costs can be eliminated, the optimal diet is no longer determined by the trade-off between reduced search time and decreasing energy gain per capture. $\bar{E}_j / \bar{T}_j$ will decrease for every size class added to the diet. In the absence of other suitable prey, and assuming there is insufficient food to satiate the predator, any item which offers a positive net energy reward should be taken, i.e. any prey type for which $E_i/TH_i>0$. Then, completion of part of the handling process by the researcher will increase the net energy value of each prey type (E_i/TH_i-- E'_i/TH'_i). The predator should now take any type for which $E'_i/TH'_i>0$.

METHODS

The data were collected between early April and mid-August of 1979, 1980 and 1981 on Mitlenatch Island, British Columbia. The island is described in some detail in Chap. II and by Butler (1974,1980). The littleneck clams are located in beds in Camp Bay (Map 2). Because of the homogeneous nature of the substrate and the low density of native littleneck clams (Protothaca staminea) in the Well Bay bed, data collection was concentrated on this area. Unless otherwise stated, mean times and sizes are given plus or minus 1 standard error.

Size distribution of clams

The size-frequency distribution of live clams was established from a series of samples located both regularly and at random over the whole clam bed. Details of this sampling procedure were given in Chapter V. Sizes reported here are the greatest over-all shell lengths measured to the nearest 0.1 mm with vernier calipers. The size-frequency distribution of clams thus generated was modified to reflect size-related differences in the availability of clams to a foraging crow. Calculation of the availability indices (Chap. VI) was based on the plan area and depth distribution of the clams and the physical parameters of the holes dug by crows. A similar approach to determining availability of subterranean prey to probing birds has been used by Hulscher (1982).

Size distribution of clams eaten by crows

The size distribution of clams eaten by the crows was established by collecting empty shells from two sources. Firstly, I retrieved the shells of individual clams as birds finished feeding from them. Secondly, a larger sample was collected in daily searches of the drop areas before they were covered by the rising tide. Only shells with some meat still adhered to them were collected, thus excluding any shells deposited by wave action.

Search and handling times

The durations of different foraging activities were measured to 0.1 s with a stop-watch. A bird returning to the beach normally landed on some prominent object, such as a boulder, before starting to search for a clam. The foraging process was then divided into six sections on the basis of the level of energy expenditure involved.

1. Searching

Timing was started when a bird hopped onto the beach from its landing spot. It searched for and captured clams by probing and digging with its bill. An extracted clam was placed on the beach and rolled into a position from which it could be grasped with its hinge distal to the gape of the crow's bill. A clam was often put down and regrasped several times, and also wiped clean of wet sand stuck to the shell, before the bird finally picked it up and flew to the drop area. The crow appeared to be 'testing' the shell for size. Frequently a clam was rejected and the bird continued searching. I noted the location of any such rejects and collected and measured them when a suitable break occurred in the foraging bout. All activities prior to take-off were considered as part of the search process, which consequently consisted of both the period required to locate a clam and a discrimination period in which its suitability was apparently assessed. Subsequent activities constituted the handling process.

2. Flight time to the first drop

Timing was started when the crow took off with a clam in its bill and was terminated when it landed after dropping the clam.

3. Handling time between drops

This consisted of the time between the crow landing from its first drop flight and taking-off to drop the clam again if it was still unbroken. During this time the crow retrieved the clam and tried to insert the tip of its bill between the valves of the shell. If the clam broke on the first attempt, timing was continued as extraction time (see 5 below).

4. Duration of subsequent drop flights

Additional drop flights were also timed from take-off to landing.

Estimates of the cost in time and energy for handling must be adjusted to account for the average number of drops needed to open a clam. Since this number may be a function of clam size, I counted the number of times a clam was dropped and then collected and measured the empty shell. The number of drops needed to open clams, outside the normal size range taken by the crows, was found experimentally by dropping 526 clams ranging from 10 to 40 mm in length onto a flat rock from heights similar to those from which crows were observed to drop them (.25 to 3.0 m, pers. obs.). Since the birds tried to open shells by pushing their bills between the valves, a clam was considered open if a finger-nail could be pushed between the valves.

5. Meat extraction time

As with handling time between drops, timing was started when the crow landed from the drop flight. When a clam was broken, the bird pulled off part of the shell and reached inside with its bill to sever the adductor muscles. The body of the clam was then pulled out and any parts still adhering to the shell were scraped out with the lateral margin of the bill. Once the bulk of the clam had been eaten the crow inspected and scraped clean any large pieces of shell which had been shaken loose. Then there was usually an abrupt change in behavior, the bird stepping away from the remains of the clam, looking round and moving unhesitatingly to another activity. Timing was terminated at this point.

To establish the effect of clam size on meat extraction time, artificially broken clams were offered to the crows on feeding tables. Clams between 10 and 40 mm were divided into six equal size classes. Ten clams from a single size class were presented each day, with the sequence of sizes offered randomized to avoid training effects. Extraction times were measured from crows feeding on these clams.

6. Flight back to the beach

Although a variety of activities (drinking, chasing, preening, courtship) followed consumption of a clam, these represent only a small proportion of a crow's time budget (James 1979). The most frequent activity was to return to the beach to look for another clam. Timing was from take-off to landing.

Manipulation of search time and prey profitability

To investigate the effect of eliminating search costs and altering prey profitability on diet choice, crows were offered clams on two plywood feeding tables. These were nailed to driftwood logs at the head of Well Bay and close to perches favored by the crows. About 30 measured clams from a day's beach sampling were placed on both tables for each trial. Over the period of the experiment, the birds thus were selecting from a size distribution of clams roughly similar to that encountered in their normal foraging. Alternate clams, in order of decreasing size, were broken so that each day the birds were confronted by equal numbers of broken and unbroken clams. Crows were allowed to feed at the tables for 2 h, after which the remaining clams were identified by remeasurement.

The ratio of the proportion of a size class in the diet to its adjusted proportion in the population was used as an index of preference (Ivlev 1961, Cock 1978). The exact value of the index for any size class is a function of diet width and the proportion of the prey population which is taken. This presents a difficulty in comparing electivity indices from different data sets. The indices from each set were therefore normalized to the average, for that set, of the indices for size classes greater than 30 mm. This assumes that clams this size are always taken when found. These normalize electivity indices were then converted to percentage mortality rates for each size class. Then probit analysis was performed using these percentages and with the numbers of prey consumed in each prey class represented by the number in that class in the samples of broken shells. An LD50 and estimates of its error limits were calculated using the methods of Finney 1962.

The crows' discriminatory powers were also tested by offering them mixtures of normal and stuffed clams on the feeding tables. Clams were stuffed with putty either to their normal weight, or to greater than the maximum observed weight for a clam of the same size, or the shells were left empty. The valves were then glued shut with epoxy resin. The mixtures of live and stuffed clams were presented to the crows for a 3 d acclimatization period and then for 6 successive days.

RESULTS

Size distribution of clams

The size-frequency distribution of live clams in the beach was established from 2,293 clams, greater than 10 mm, found in the sampling process (Fig. 18). The distinctive peak around 14 mm corresponds to the previous year's recruitment (Fraser and Smith 1928, Quayle and Bourne 1972, Paul and Feder 1973). Sampling over the period of maximum growth and the relatively slow growth rate of this species has obscured the distinction between other age classes. However, sampling throughout the period of predation by the birds probably resulted in a more realistic size frequency distribution than the static one resulting from a single large sample. The size distribution corrected for size specific availability to foraging crows is also shown in Fig. 18. There is, in fact, little difference

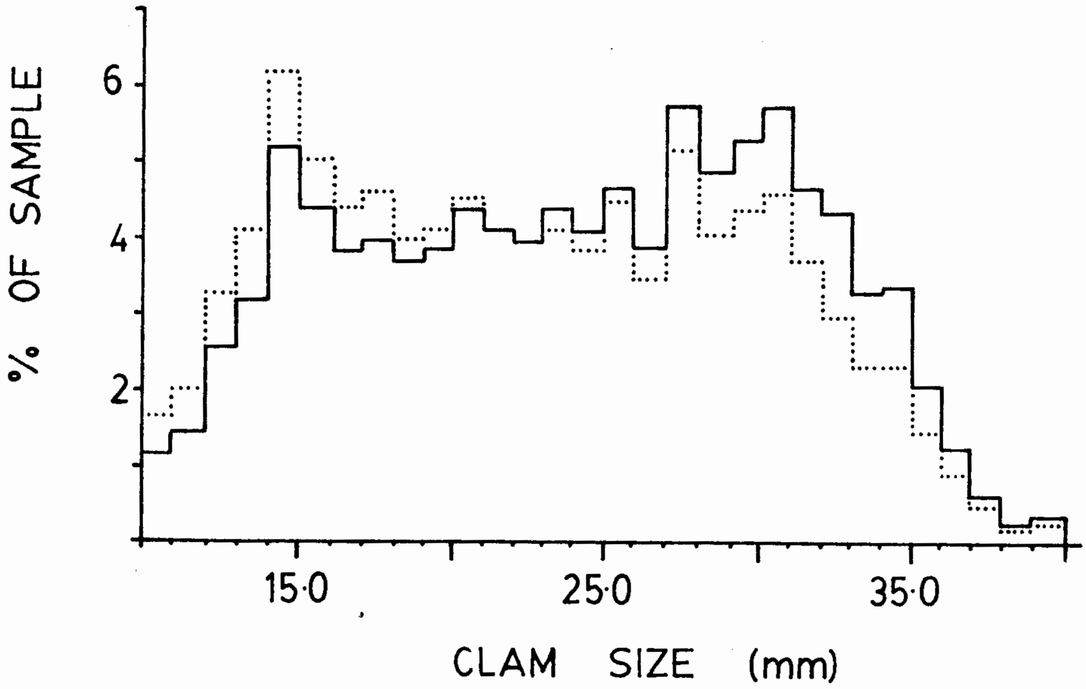


Fig. 18. Size-frequency distribution of 2293 live clams from Well Bay samples (....) and the distribution corrected for size dependent availability to crow predation (——).

between the two size distributions. Large clams are more likely to be encountered because of the large plan area which they present to a searching crow, but they are also deeper in the substrate at a level to which fewer of the crows' probes penetrate.

Size distribution of clams eaten by crows

The mean size of 457 shells located immediately after a crow had finished feeding on them was 32.7 ± 0.15 mm. That of 2808 shells collected in daily searches of the drop areas was 32.6 ± 0.05 mm. As there is no significant difference between these two samples ($t = 0.2$, $df = 3264$, $P > 0.5$), the collection from the drop area was concluded to be representative of the clams eaten by the crows, and the size-frequency distribution was established from the pooled samples (Fig. 19). Evidently crows did not feed on the smaller clams. Possible reasons for the under-representation of these clams in the crows' diet will be discussed later. That they did in fact encounter smaller clams is shown by the size distribution of 514 rejected clams (Fig. 19). The mean size of these rejects was 27.6 ± 0.16 mm. In 115 cases it was possible to find both rejects and the shell of the clam that the crow ultimately ate. The total number of rejects for these 115 clams was 298. In only 14 cases was the clam eventually eaten smaller than one of the foregoing rejects, and in only 3 cases was the difference more than 1 mm. Given that the birds may be estimating size on the basis of weight or

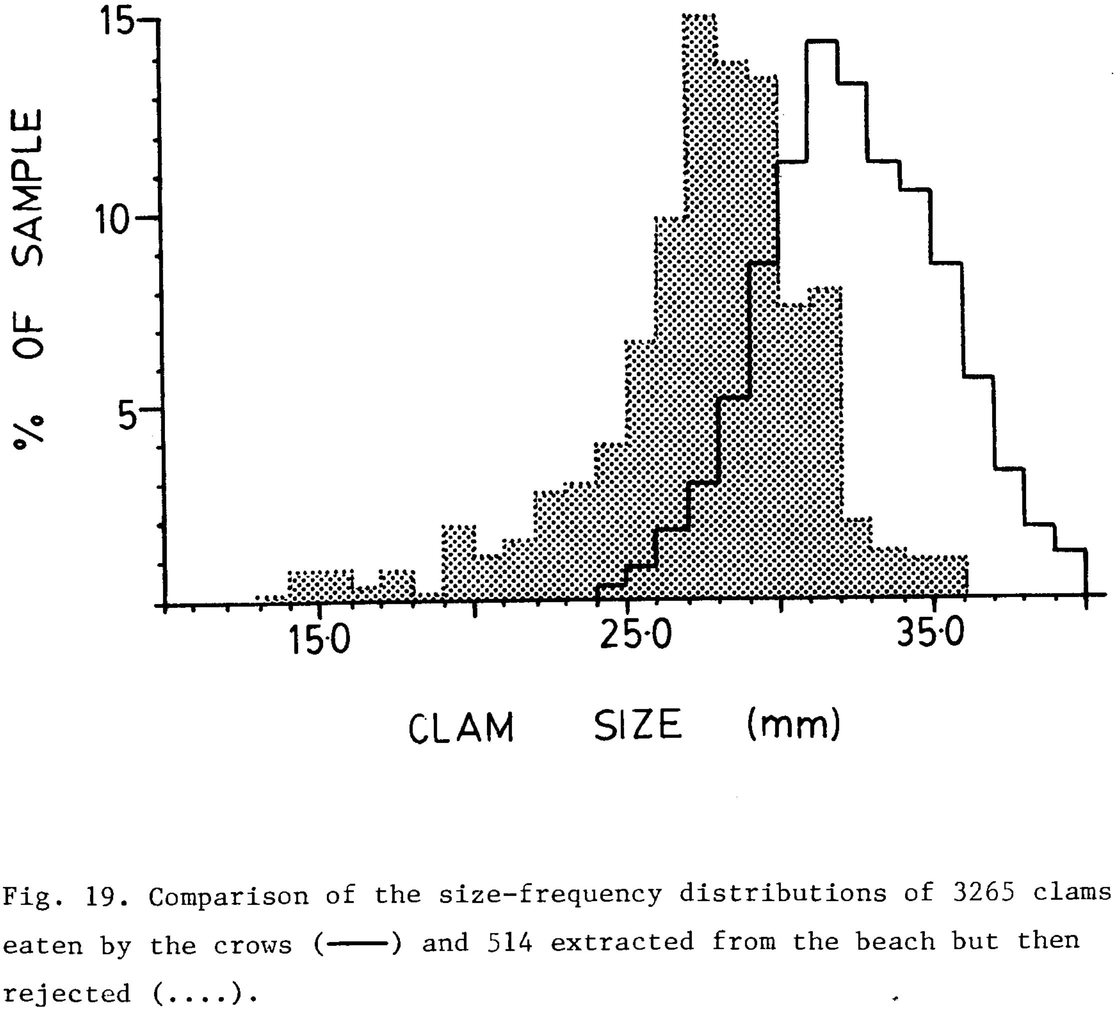


Fig. 19. Comparison of the size-frequency distributions of 3265 clams eaten by the crows (——) and 514 extracted from the beach but then rejected (....).

width, rather than length, it appears that they are capable of considerable consistency in judging clam size.

The normalized electivity indices for the full range of clams available (Fig. 17) show that the crows had a partial preference for clams of intermediate size. Clams between 24 and 31 mm were neither always taken nor always rejected. The level of 50% preference (LD50 from the probit analysis) was used as a single size class estimate of the lower limit of the observed diet for an average bird. This was at approximately 29.0 mm.

Search and handling times

1. Searching time: TS_j and TS_x

   The mean duration of 186 searches was 34.6 ± 4.09 s. The previously calculated lower limit to the diet of 29.0 mm and this observed search time (TS_x) were then used to predict search times for the full range of hypothetical diet widths (TS_j for all values of j). It is assumed here, and will be established later, that profitability is an increasing function of clam size.
2. Flight time to first drop

   The duration of all drop flights was assumed to be independent of clam size. The mean duration of 80 first drop flights was 4.2 ± 0.64 s.
3. Handling time between drops

   The duration of this activity was also assumed to be independent of clam size. Because of the short duration and comparatively low energetic cost of the constituent activities, errors introduced by this assumption should be minimal. The mean duration of 95 handling times between drops was 5.5 ± 0.55 s.

4. Duration of subsequent drop flights

The average flight time of 96 second drops was 2.0 ± 0.24 s. The number of clams requiring one, two, or more than two drops to break is shown for 385 naturally (Table 12) and 526 experimentally (Table 13) broken clams. There was no significant relationship between the size of clams and the number of drops required to break them, in either natural ($X^2 = 10.58$, df = 4, $P > 0.5$) or experimental ($X^2 = 15.0$, df = 10, $0.5 > P > 0.1$) groups. Close agreement between the average number of drops needed to break clams by the experimental method (1.63 drops/clam) and the number observed in the drop zone (1.71 drops/clam) indicates that my method was consistent with that used by the crows. The duration of handling between drops and for subsequent drops was therefore adjusted to reflect the observed average of 1.71 drops/clam.

5. Meat extraction time

The average time to remove the meat from the shells of each experimental size class is shown in Fig. 20. Also shown is the mean time for each size class of clam recovered from normally feeding birds. The regression equation

$$\text{Extraction time (s)} = 0.13\ (\text{clam length})^{1.58}$$

was calculated from the pooled data.

6. Return flight to the beach

The mean duration of 100 flights back to the clam beds was 3.6 ± 0.27 s, significantly shorter than the average duration of flights from the clam bed to the drop area ($t = 8.45$, $df = 178$, $P < 0.001$). I think this difference is due to the height gain and maneuvering involved when dropping a clam, rather than to the increased load from carrying it.

Prey profitability

The relationship between clam size and the weight of its soft parts, dried at 65 C to constant weight, was:

$$\text{dry weight(mg)} = 0.016(\text{clam size})^{3.47} \quad (n = 130,\ R = .95)$$

The value of 20.0×10^3 J/g dry wt. was used to calculate the gross energy content of each size class. This figure is similar to the measured caloric value of a variety of other invertebrates (Cummins & Wuycheck 1971, Menge 1972, Prus 1970). Values of E /TH were then calculated from the observed handling times, a basal metabolic rate of 3.6 J/s (Irving *et al*. 1955), an assimilation efficiency of 70% and multipliers (see Table 14) of 9BMR for flying, 4BMR for searching and 2BMR for other parts of the handling process (Zach 1978 and refs. therein). The cost of searching used here is higher than that used by Zach (3 BMR) because the crows in his study were searching for prey located on the surface. In digging for clams a crow must expend

Table 12. Frequency of the number of drops needed by crows to open clams of different sizes.

Number of	Clam size (mm)			
drops	<30.0	30.0-34.9	>35.0	Total
1	46	127	60	233
2	14	46	28	88
> 2	15	31	18	64
Totals	75	204	106	385

$X^2 = 1.58$, df = 4, $p > .50$

Table 13. Frequency of the number of experimental drops needed to open clams of different sizes. Clams were dropped by hand from heights ranging from 0.5 to 3 m onto a flat rock. Sizes given are the mid-range points.

Number of	Clam size (mm)						
drops	12.5	17.5	22.5	27.5	32.5	>35.0	Total
1	16	61	90	88	78	36	369
2	9	27	22	15	16	7	96
> 2	4	11	11	12	15	8	61
Totals	29	99	123	115	109	51	526

$X^2 = 15.0$, df = 10, $.5 > p > .1$

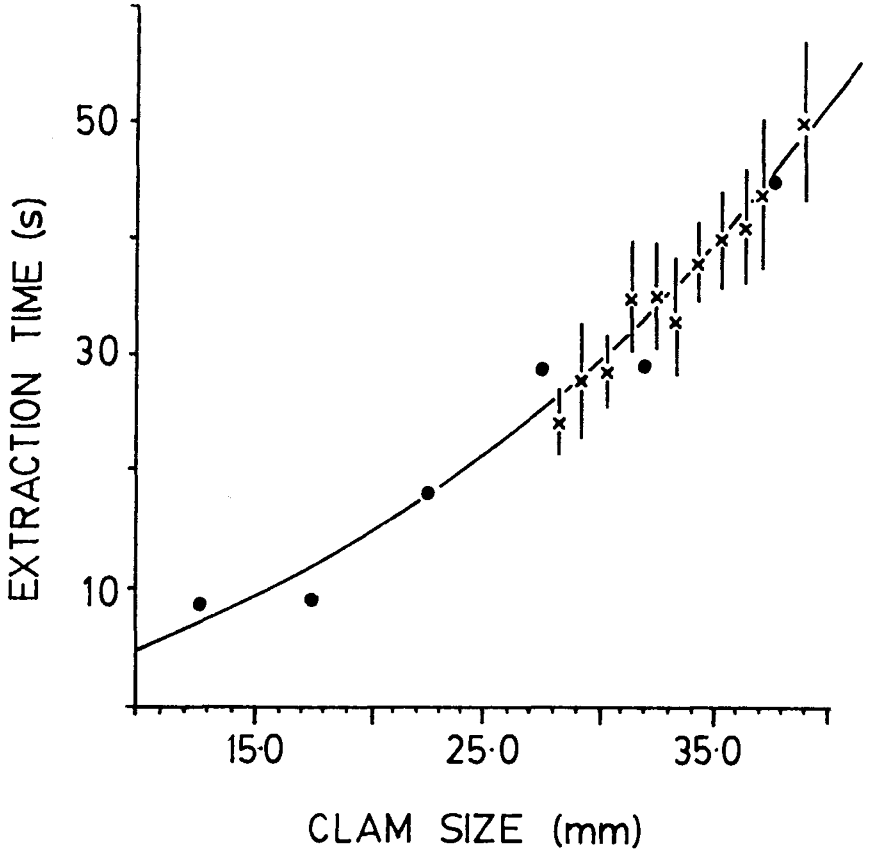


Fig. 20. Mean time required (± S.E.) to extract meat from broken shells by birds feeding on the beach (x) and on the feeding tables (●) as a function of clam size. The regression equation: Extraction time (s) = 0.13 x (clam size)$^{1.58}$ was calculated from these 17 data points.

considerably more energy than when turning over seaweed looking for surface prey. It was assumed that the energy expended in flight was independent of the size of clam being carried. This is reasonable as even the largest clams eaten weigh only about 20 g, or approximately 5% of the body weight of an adult crow. Fig. 21 shows E_i/TH_i to be a uniformly increasing function of clam size. The ranking of prey therefore should be from high-quality, large, to low quality, small clams. Also shown in Fig. 21 are values of E'_i/TH'_i, calculated by subtracting the time and energetic costs of breaking clams from the E_i/TH_i values. An unbroken clam less than 17.5 mm does not provide enough energy to cover the cost of handling. When most of the handling process was experimentally completed by breaking the clams, even the smallest yielded a positive net reward. It was predicted, therefore, that crows should take any broken clams offered on the feeding tables and any unbroken ones of 17.5 mm or larger.

The time spent on each part of the foraging process and the estimated energy expenditure for each activity is summarized in Table 14.

Energy gain per capture and the optimal diet

Rates of energy intake per prey capture for all possible diet widths were calculated by sequentially adding smaller size classes to the diet. The relationship between the rate of energy gain and diet width is shown in Fig. 22. A crow feeding on only

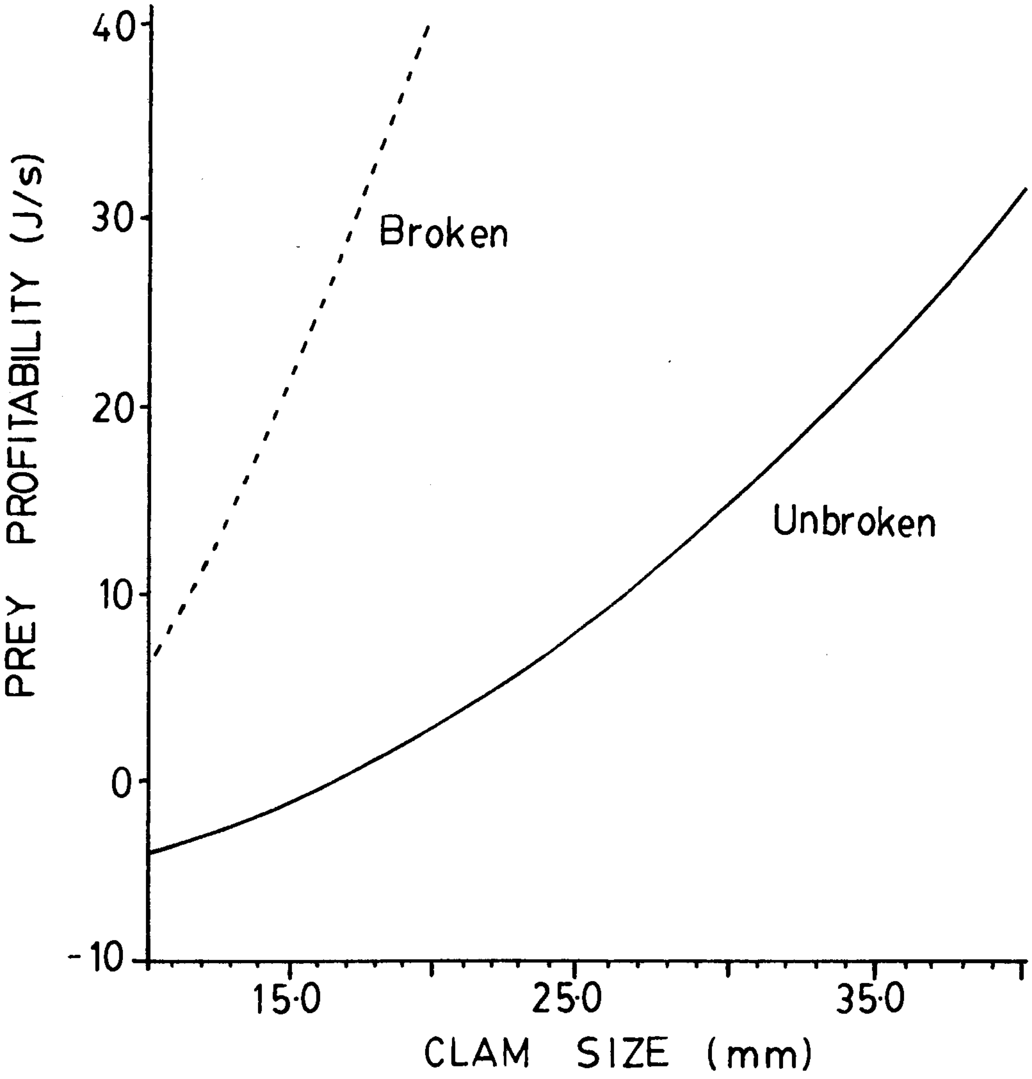


Fig. 21. Profitability of both unbroken (E_i/TH_i) and broken (E'_i/TH'_i) clams to a crow taking them from the feeding tables, as a function of clam size.

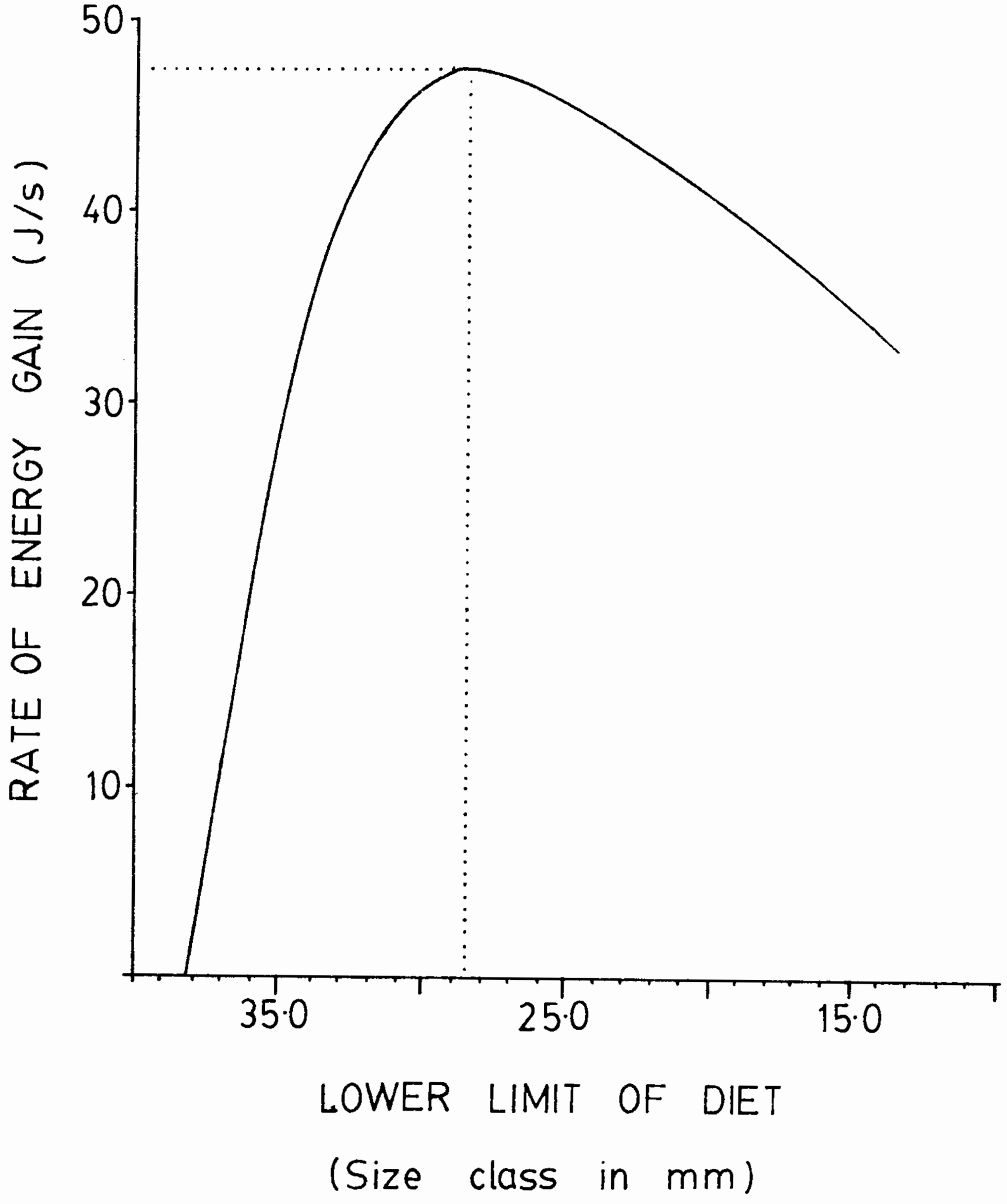


Fig. 22. Average rate of energy gain per capture as a function of diet breadth. The maximum rate of 47 J/s occurs with a diet including all clams of 28.5 mm or larger.

Table 14. Summary of the mean durations and energetic costs of activities performed by northwestern crows in finding and eating littleneck clams.

Activity	n	Times (s)	Energy (J)
Searching (TS_x)	186	34.6 ± 4.09	485 (4 BMR)
Flight to first drop	80	4.2 ± 0.64	134 (9 BMR)
Between drops	95	5.5 ± 0.55	43 (2 BMR)*
Second drop	96	2.0 ± 0.24	70 (9 BMR)*
Extraction time (calculated from)		$0.13(\text{clam length})^{1.58}$	and 2 x BMR
Return flight	100	3.6 ± 0.27	115 (9 BMR)

*Energy costs based on 1.71 drops/clam

the highest quality clams (> 38 mm) would be expending more energy searching than could be recouped by its infrequent captures; $\bar{E}_j/\bar{T}_j$ is actually negative. The rate of energy acquisition increases rapidly with the addition of clams down to 33 mm. The shape of this part of the $\bar{E}_j/\bar{T}_j$ curve is dominated by the rapidly increasing frequency (Fig. 18) of clams in each successive size class which is added to the diet. Normally there is a dilution effect on the change in search time with each additional prey type. If all sizes were equally numerous, adding a second size to a diet containing only the highest quality prey would decrease search time by half, while adding a sixth size class to a diet already containing five reduces it by only one fifth. In the system discussed here this effect is masked by the increasing frequency of clams between 40 and 30 mm (Fig. 18).

The maximum energy intake rate of approximately 47 J/s is achieved by taking clams 28.5 mm or larger. The inclusion of more size classes has only a small effect on the rate of energy gain. This is partly because of the afore-mentioned dilution effect and partly because of the exponential nature of the E_i/TH_i curve. With relatively little difference between the net energetic value of size classes between 20 and 10 mm, the average energy gain per capture changes little with each class added to the diet. The 28.5 mm predicted lower limit to the optimal diet is only 1.3 times the standard error of the observed 29.0 mm limit for crows feeding on the beach.

Clams taken from the feeding table

Approximately a dozen birds came readily to the feeding tables, and typically took the largest available clam first. Unbroken clams were carried to the drop area, a distance similar to that between the clam beds and the drop area. Birds taking large pre-broken clams hopped or flew a short distance to a convenient log. Small broken clams were eaten on the table.

There is a significant difference between the size distributions (Fig. 23) of broken and unbroken clams taken (Wilcoxon 2 sample test, $t = 3.06$, $P < 0.01$). The normalized electivity indices for broken and unbroken clams from the feeding tables and for clams taken from the beach are shown in Fig. 24. The 50% preference level is again used as an approximation of the lower limit to what the birds will take in each situation. The smallest clams taken by crows feeding on the beach are 29.0 mm. This drops to approximately 22.0 mm for unbroken and 14.0 mm for broken clams when feeding at the tables. The calculated values were 19.5 and 11.5 mm respectively. Both these values are more than 5 standard errors from the 50% preference measures and therefore cannot be considered as good approximations.

As the crows take clams roughly in order of decreasing size (and profitability), there is a concomitant decrease in the rate at which energy is obtained from this source. The decision to leave the tables, the timing of which would determine the smallest size clams taken, may be due to the presence of an

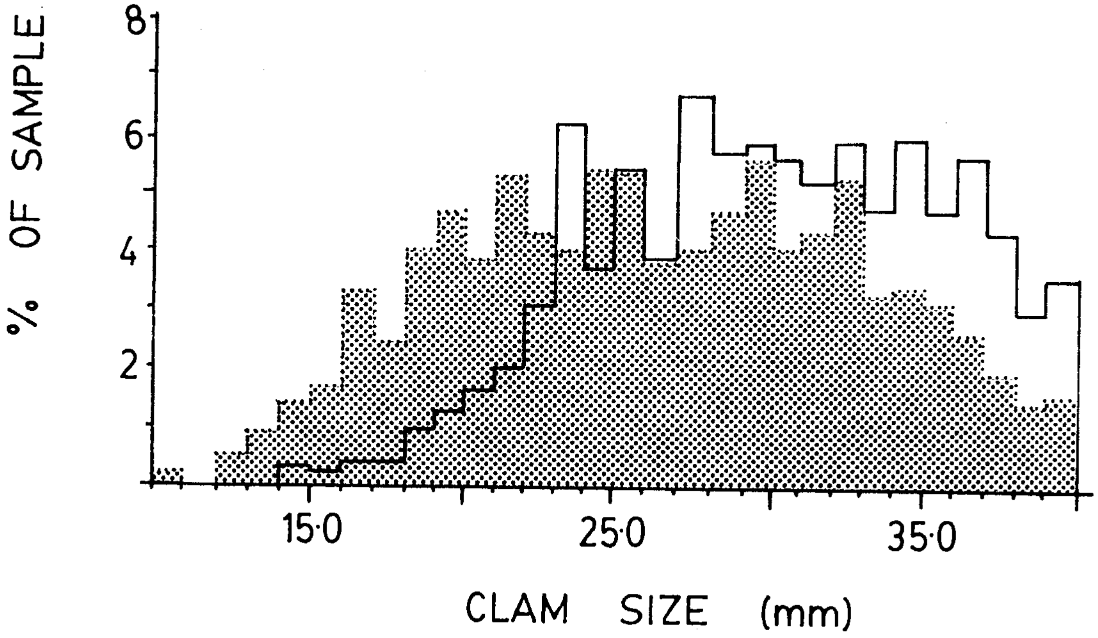


Fig. 23. Comparison of the size-frequency distributions of 570 unbroken (-----) and 563 broken clams (.....) taken by crows from the feedinf tables.

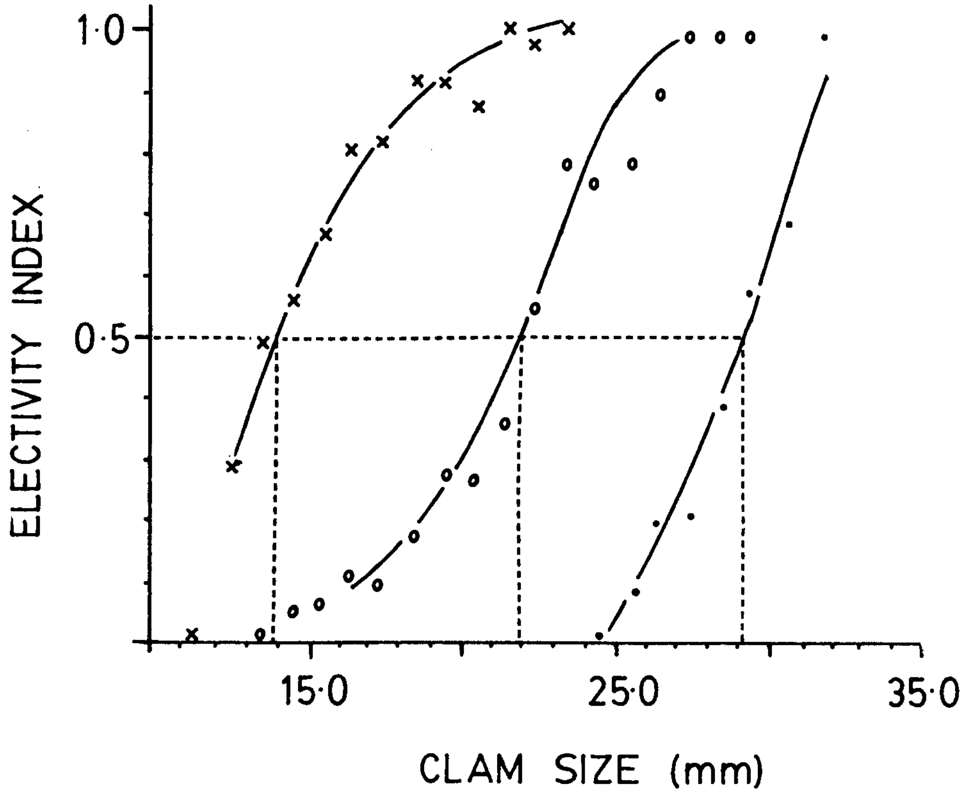


Fig. 24. Normalized electivity indices for clams taken from the beach (.), and for unbroken (o) and broken clams (x) taken from the feeding tables.

alternative, more rewarding food source. As the trials were run during afternoon high tides, the only other potential foods were insects from the meadows and eggs, excreta and regurgitated food from the gull colony (Butler 1974, 1980). After feeding at the tables the birds usually ignored these other sources of food and remained near the tables preening, resting and occasionally recovering stored clams. The consumption of stored clams makes it unlikely that the birds stopped taking clams from the tables simply because they were satiated. Such clams deteriorate only slowly and are rarely found by other crows (James 1979, James and Verbeek 1983), so their net worth remains the same no matter how long the birds continue to feed at the tables. The maximum long term benefit from these caches would be obtained by feeding on them only when other sources are exhausted or unavailable. Therefore, they were not considered as an immediate alternative to clams on the feeding tables. The difference between the minimum sizes of broken and unbroken clams taken is undoubtedly real since these selections were made simultaneously.

Crows are clearly able to distinguish between normal and abnormal weight clams. They took nearly all (65/67) normal weight clams presented to them on the feeding tables, but only a small proportion (5/47) of the light and heavy ones (Table 15). The fact that they took all the normal weight stuffed clams rules out the possibility that this choice was made on the basis of changes resulting from the stuffing proccess.

Table 15. Comparison of the numbers of live and stuffed clams taken from the feeding tables. Light clams were empty shells glued together. Normal and heavy stuffed clams were filled with plasticene to the mean or greater than the 95% confidence limit of the mean weight for live clams of equal length. All clams were within the size range normally eaten by crows.

	Live clams	Stuffed clams		
		Light	Normal	Heavy
Taken	55	1	10	4
Remaining	2	24	0	18
Totals	57	25	10	22

DISCUSSION

The aims of this chapter were to calculate the optimal size range of clams on which crows should feed and to compare it with the range of clams actually eaten, and secondly to test the ability of the birds to assess the energetic value of different prey sizes.

Several authors (Schluter 1981, Zach and Smith 1981) have questioned the usefulness of optimality theory in field studies, arguing that the situations involved are generally too complex for the researcher to make valid predictions of optimal behavior, against which to measure the actual performance of the predator. It is suggested here, that although this may be the case for many predator-prey systems, there are other situations with sufficient spatial or temporal separation of prey types, that the generation of such optima is both theoretically realistic and practically feasible. The crows on Mitlenatch do utilize a number of different food sources (Butler 1974,1980) but the clam beds are spatially distinct from any other source. Clams represent by far the largest proportion, both numerically and particularly volumetrically, of food taken from the beds (Chap. IX). It therefore seems reasonable to ask what size range of clams the crows should eat to achieve the optimal solution to some particular problem.

What to optimize?

The first question to address is whether maximization of net energy gain is that problem. The data presented here were gathered during the crows' breeding season and there is strong evidence to suggest that they were energetically limited during this period. A 5-yr breeding study of the crows on Mitlenatch Island (Butler 1980, Verbeek, Butler & Richardson, M.S.) has shown that the most common clutch size is four eggs. Although as many as 80% of the eggs hatch, only 30% of the nestlings fledge. This level of fledging success is amongst the lowest for passerines (Lack 1954). The main cause of chick mortality appears to be starvation. By comparing the last recorded weight of a chick to its own weight over the previous 3 d, or to that of young of the same age which subsequently fledged, 43 out of 57 (75%) dead chicks were judged to have starved. During incubation and the early nestling period the female remains on the nest almost continuously and the male provides most of the food for both his mate and the nestlings. At a minimal energetic expenditure of 1.5 x BMR, the female's daily requirement is about 4.7×10^5 J or nearly 3 h of continuous clamming for an optimally foraging mate. It would obviously be beneficial for the male to forage as efficiently as possible.

An alternative possibility is that the crows select their diet to optimize the intake of some other nutrient factor. The energy content of the clams was calculated as a simple power function of weight, and the relationship between most other body constituents and size will probably be very similar to this. Because of this assumed covariance, maximization of energy intake will neccessarily involve the simultaneous maximization of the intake of many other nutrients. Irregularities in such relationships are most likely to occur with changes in the clams' reproductive status. The Japanese littleneck clams on Mitlenatch grow at rates roughly the same as both Japanese and native littlenecks from other Vancouver Island populations (Fraser and Smith 1928, Feder and Paul 1973, pers. obs.), becoming sexually mature at 2 or 3-yr, or between 22 and 35 mm long (Quayle 1943). While this range does coincide with the range of partial preference exhibited by the crows (Fig. 17), optimization of the intake of some constituent of mature clams is complicated by the fact that individuals are single sexed. Compositional changes during reproduction are likely to be sex specific, but the sexes are externally monomorphic. The converse, that the crows may be trying to minimize the intake of some component of smaller, immature clams is unlikely considering their willingness to feed on even the smallest clams in the experimental situations.

It therefore seems that maximization of the rate of energy intake is the probable aim of a crow in selecting its diet.

Can crows assess prey quality?

Optimal diet theory requires that predators be able to rank prey in order of profitability. Stenseth and Hansson (1979) have argued that one of the weaknesses of this theory is the lack of evidence for any such ability. Emlen and Emlen (1975) suggest that not only are errors in the decision making proccess to be expected, but that they will obscure the precise boundaries of the diet. Several lines of evidence show that crows can assess and rank prey profitability and that they do so with reasonable accuracy. From the collection of 298 rejected clams, only 14 were larger than the clam which was eventually taken, and in most cases the difference was minimal (< 1 mm). The crows can also detect clams of abnormal weight, as demonstrated by their rejection of empty and heavy stuffed shells on the feeding tables. In an analogous natural situation crows occasionally find the closed shells of dead clams filled with sand. During measurement I have handled such clams without realizing they were not live yet, of the thousands of clams which I saw crows drop, none were sand filled. Finally, the extension of their diet width to include normally non-preferred sizes shows that the crows do perceive, and assess the extent of, the experimentally induced changes in net reward.

Are crows selective?

A number of studies (Davies 1977, Hulscher 1982, Sutherland 1982, Turner 1982) have shown that birds apparently feed selectively and thereby achieve a rate of energy intake greater than would be expected from taking all prey items as they are randomly encountered. Unfortunately, in most of these studies the predator is assumed to encounter each prey class in the same proportions as the researcher. Rarely do biologists and their research animals sample prey populations with the same methods and it is therefore difficult to distinguish between selective feeding and differential availability of prey types. In this study the relative proportion of each prey size class has been adjusted to reflect the foraging methods of the crows (Fig. 18) and hence strengthen the argument for selective predation. Also, the unique occurrence in this study of an actual physical rejection of some clams, provides concrete evidence of a size range of prey (Fig. 19) which are found and 'captured' by the crows but then abandoned in favor of searching for larger ones. Consequently, the assertion that crows feed selectively on the largest and energetically most rewarding clams can be made here with more conviction than in most other diet selection studies. There is still an obvious discrepancy between the clams available (Fig. 18) and the sum of the rejects and those eaten by the crows (Fig. 19). However, it is suggested that the size of the smallest clams can be judged _in situ_, while that of clams close to the limit of acceptability must be assessed on the surface for greater accuracy. In support of this is the number of small clams (< 20 mm) that were clearly visible on the bottom or in the sides of many of the holes dug by the crows.

As in many optimal diet studies (Emlen and Emlen 1975, Goss-Custard 1981, Krebs _et al_. 1977, Werner and Hall 1974), selectivity is not as precise as predicted by theory, there being a size range of about 8 mm for which the crows showed a partial preference (Fig. 19,24). This is not unexpected in a field study, as the all-or-none consumption predicted by optimal diet models (Pyke _et al_. 1977 Krebs 1978, Goss-Custard 1981) is based on the somewhat unrealistic premise that predators do not vary in their ability to detect, capture and handle prey. On Mitlenatch Island yearling crows were considerably less efficient foragers than adults (Chapter VIII), and a few individuals used quite different feeding methods from the majority. One aggressive adult invariably landed next to a crow which had already dug a hole, chased it off and looked for a clam in the pre-dug hole. Three others, two yearlings and an adult, often dropped two clams at a time. Such differences in foraging technique and prey handling ability will alter the net reward of each size class to individual birds and thus influence their choice of diet. Lumping the data from a number of birds will neccessarily obscure what may otherwise have been well defined limits to the diet of individual birds.

Pooling the data from single birds gathered at different times in the summer could produce the same result. Predation and growth may influence the availability of preferred size classes, and thus, the diet choice of individual birds over time. However, predation probably has a minimal effect on clam density which is locally as high as 400 clams larger than 25 mm per 1 m^2, while the period of most rapid clam growth is in the first 2 yr, or in clams outside the crows′ normal diet range. An analysis of the size distribution of the daily shell collections showed variance to be constant (Bartlett test for homoscedasticity, $X^2 = 21.96$, df = 32, $P < 0.01$) and no significant relationship between mean size and date (Anova, F = 2.13, df = 20, $P < 0.005$). Prey density is therefore assumed to be relatively constant (see Chap. V).

The arbitrary use of clam length and of 1 mm size classes may also exaggerate the extent of partial preference. Measuring clam size with vernier calipers perhaps produces a degree of accuracy unmatched by the crows using their bill or eyes. This would introduce an artificially high level of resolution to the data analysis. Alternatively, using width or weight as the measure of clam size, may produce a more sharply defined lower limit to the diet.

Is the crows diet optimal?

Agreement between the range of sizes of clams eaten by crows in different situations and that which they were predicted to take under an energy maximization hypothesis (Table 16), is too close to be coincidental. In fact, the agreement reported in the results can be improved by adjusting some of the estimated parameter values incorporated in the calculations. For instance, using a BMR of 4.18 J/s, 18.8×10^3 J/g dry wt. and multipliers of 10 BMR for flight and 3 BMR for handling, the predicted minimal size of unbroken clams which the crows should take from the feeding tables is 19.5 mm. That for broken clams becomes

11.5 mm (Table 16). While other equally reasonable parameter values will decrease the agreement between observed and predicted values, this does illustrate that the small discrepancies observed may be the result of errors in these parameter estimates.

There seem few species more likely to possess the sophisticated discriminatory powers required for efficient diet selection than the crow, with its highly catholic tastes in food. Shellfish offer high energy yields, yet the need to drop them to break them open requires a considerable initial energetic investment. The use of this tactic by northwestern crows to deal with such diverse items as whelks (*Thais lamellosa*), littleneck clams, mussels (*Mytilus* sp.), oysters (*Crassostrea gigas*), red rock crabs (*Cancer productus*), a variety of nuts and even a gull head (pers. obs.) could lead to a diet far from the energetic optimum were the birds not discriminatory.

Table 16. Comparison of the minimum size clams predicted and observed to be eaten by northwestern crows in both natural and experimental situations. Values given in brackets were calculated from alternative parameter values discussed in the text.

	Minimum size (mm)	
	Predicted	Observed
Well Bay clam bed	28.5	29.0
Feeding tables:		
unbroken	17.5 (19.5)	22.0
broken	10.0 (11.5)	14.0

VIII. DIET SELECTION BY YEARLING CROWS

INTRODUCTION

A number of species of birds gain access to the edible parts of hard shelled prey by dropping them (Barash *et al*. 1975, Kent 1981, Maron 1982, North 1948, Oldham 1930, Priestley 1947, Tinbergen 1953). When using this technique a predator must make a number of decisions if it is to gain the maximum net energy return for its effort. It must choose the right substrate on which to drop the prey (Barash *et al*. 1975, Siegfried 1977, Zach 1979), the height from which to drop it (Maron 1982, Siegfried 1977, Zach 1979), how many times to drop it before giving up if it does not break (Zach 1979) and which sizes of prey to drop (Kent 1981, Zach 1979, see also Chap. VI).

Immature individuals of a number of species perform such complex tasks less efficiently than adults (Barash *et al*. 1975, Buckley and Buckley 1974, Dunn 1972, Maron 1982, Orians 1969, Recher and Recher 1969, Siegfried 1977, Verbeek 1977), thereby achieving a reduced net energy intake per capture. Consequently, the diet which maximizes this rate for an inefficient forager, will incorporate a wider range of prey items (Ebersole and Wilson 1980). I have shown (Chap. VII) that adult northwestern crows (*Corvus caurinus*), feeding on littleneck clams (*Venerupis japonica*), obtain close to the theoretical maximum energy yield, with a diet consisting of clams greater than 29.0 mm. The aims of this chapter are to compare the efficiency of adult and yearling crows in handling littleneck clams, to establish the diet breadth of yearling crows and to calculate the rate of energy intake which they could expect to gain by taking any other size range of clams.

METHODS

The data were collected from late-April to early-August, 1981 and 1982 on Mitlenatch Island, British Columbia, more detailed descriptions of which can be found in Chapter II and Butler (1974,1980). The size-frequency distribution of live clams in the beach in 1981 was determined from 202 sample quadrats, each 25 by 25 by 15 cm, spaced at regular 3 m intervals over the whole clam bed (Chap. V). The size-frequency distribution of clams eaten by the yearlings was established by collecting empty shells immediately after the birds had finished feeding from them. Search times were measured throughout the summer of 1981 and handling times in 1982 by the methods described for adults (Chap. VII). Details of the methods of calculating the size specific availability of clams to foraging crows and the optimal diet are given in Chapters VI and VII, respectively.

Yearling crows are otherwise morphologically similar to adults but can be identified by the brown cast to their plumage, particularly on the wing tips and tail coverts (Verbeek and

Butler 1981). Yearlings are birds in their first full spring and summer, prior to molting into full adult plumage.

RESULTS

Availability of different size clams to yearling crows

When searching for clams, yearlings used a similar proportion of digs to probes as adults (Table 17) and the frequency distributions of the depth of digs made by both was the same (Fig. 25). In contrast, a significantly smaller proportion of the probes made by yearlings penetrated to more than half a bill length (Fig. 26). However, this difference had only a minimal effect on the relative availability of different size clams. Why yearlings made fewer deep probes is uncertain. If this were due to a lack of strength or technique, they should have resorted to digging more often. Alternatively, if they were pecking at surface objects which adults ignored, a higher proportion of probes to digs would have been expected.

Size of clams eaten by yearling crows

The size range of 174 clams eaten by yearlings was 22 to 39 mm; very similar to the range of 23 to 42 mm for 575 clams eaten by adults and collected concurrently (Fig. 27). However, the median size of clams eaten by yearlings (31.3 mm) was significantly smaller (Mann-Whitney U test, $P < 0.001$) than the

Table 17. Comparison of the proportions of probes and digs used by adult and yearling northwestern crows searching for littleneck clams in Well Bay. Sample sizes are given in brackets.

	Proportion of all searches	
	Adults	Yearlings
Probes	.55 (353)	.60 (339)
Digs	.45 (289)	.40 (230)

$X^2 = 2.62$, df = 1, $0.5 > p > 0.1$

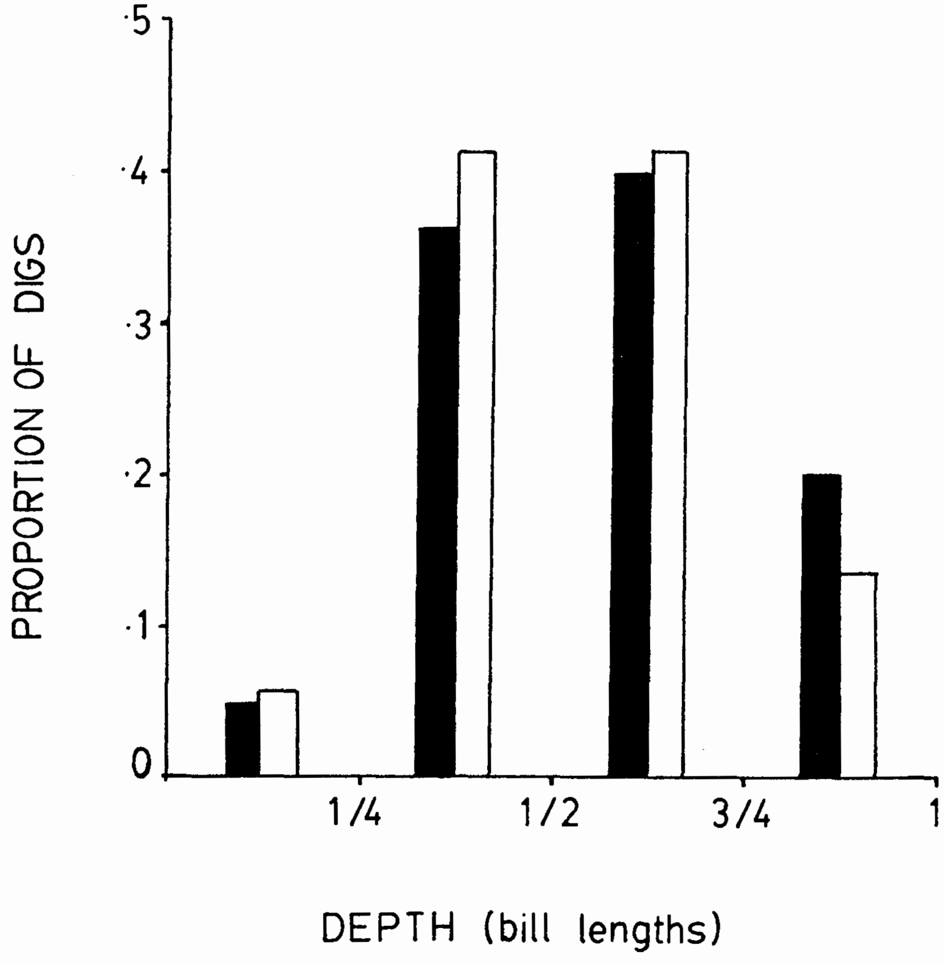


Fig. 25. Comparison of the depth-frequency distributions of 289 digs made by adult (solid bars) and 230 made by yearling (open bars) northwestern crows searching for littleneck clams in Well Bay.

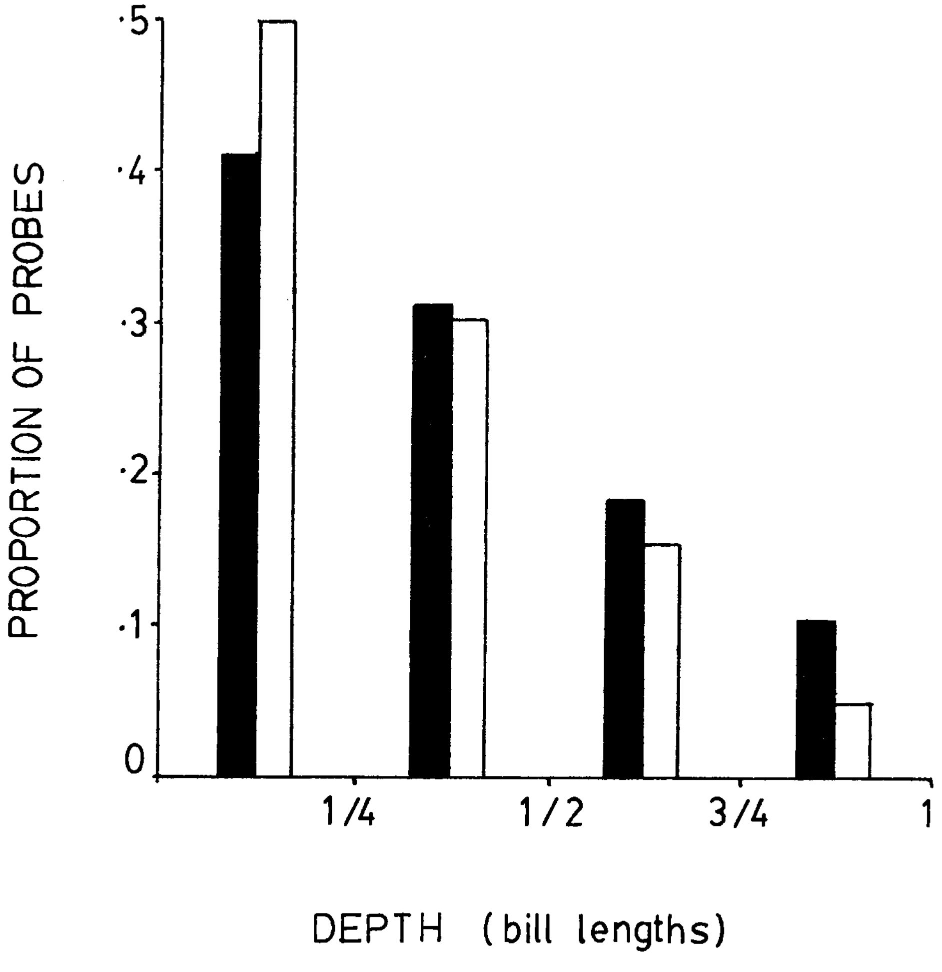


Fig. 26. Comparison of the depth-frequency distribution of 353 probes made by adult (solid bars) and 339 made by yearling (open bars) northwestern crows searching for littleneck clams in Well Bay.

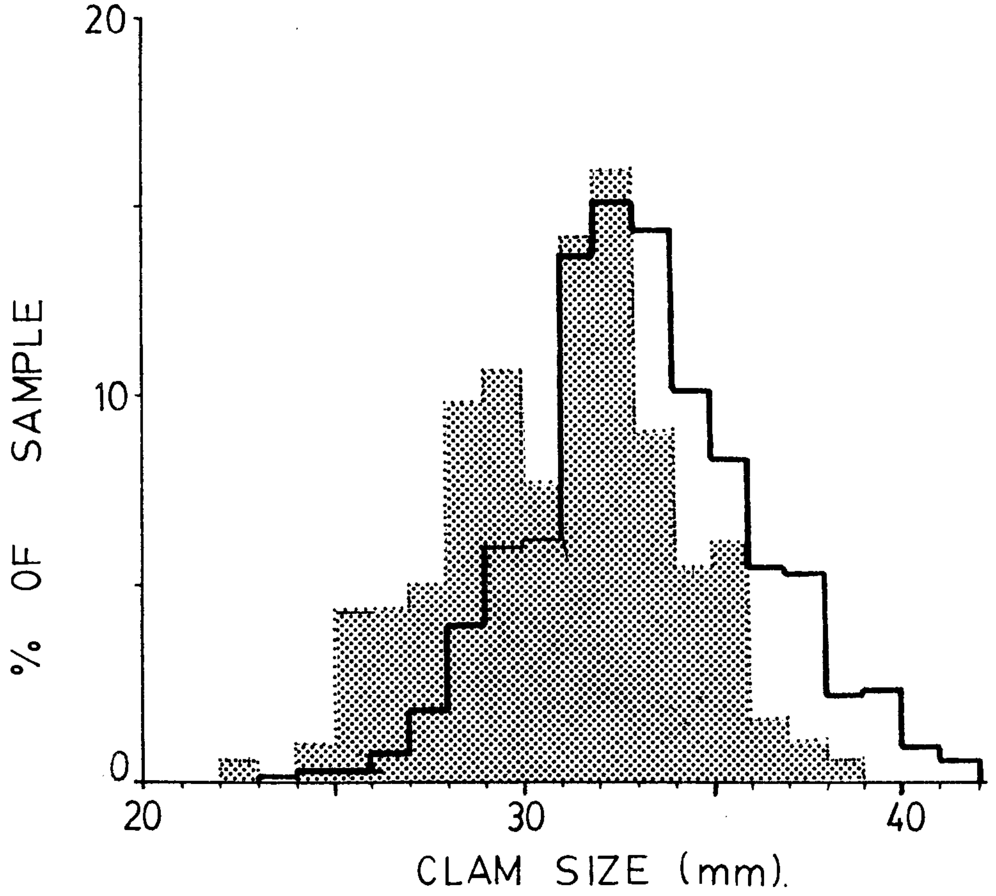


Fig. 27. Comparison of the size-frequency distribution of 575 littleneck clams from Well Bay eaten by adult (——) and 174 eaten by yearling (....) northwestern crows.

median of those eaten by adults (33.0 mm). Electivity indices (Ivlev 1961) were calculated for all size classes. For comparative purposes these were normalized to the mean of the indices for clams between 32 and 36 mm (Chap. VII). It was assumed that clams in this size range were taken whenever encountered. The size range of clams rejected by yearlings (Fig. 28) supports this assumption. Size classes above 36 mm represented a proportion of the population too small for accurate calculation of the indices. The 50% preference level, presumed to represent the behavior of the average yearling, was used as a single size class estimate of the lower limit of the diet. This was approximately 25.5 mm (Fig. 29) compared to 29.0 mm for adults (Chap. VII). Because the calculations for yearlings were based on a small number of clams, there is greater variation in the electivity indices than in those for adults. This reduces the accuracy of the estimate of the lower limit of the diet. However, the size-frequency distribution of clams taken by the yearlings (Fig. 27) clearly indicates that they did feed on a greater proportion of small clams than did adults.

Duration of search and handling times

Yearlings spent significantly more time to complete every part of the search and handling process than adults, except to fly from the drop zone back to the clam bed (Table 18). They also required an average of 2.0 drops to break open clams,

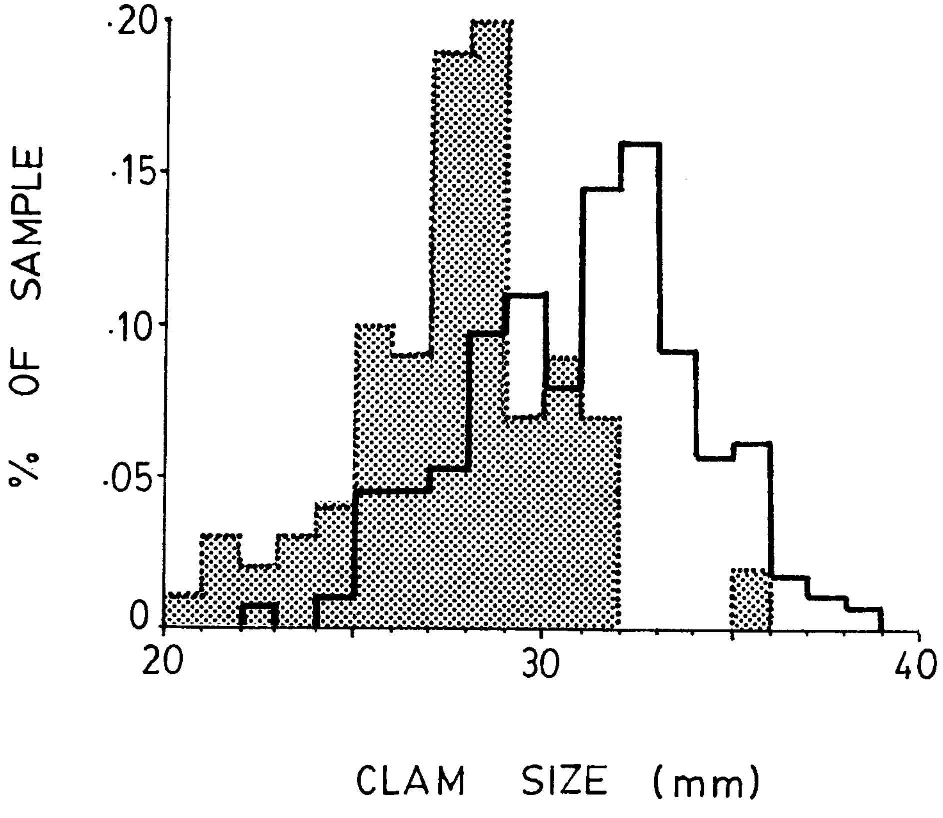


Fig. 28. Comparison of the size-frequency distributions of 174 littleneck clams eaten (——) and 98 clams rejected (....) by yearling northwestern crows.

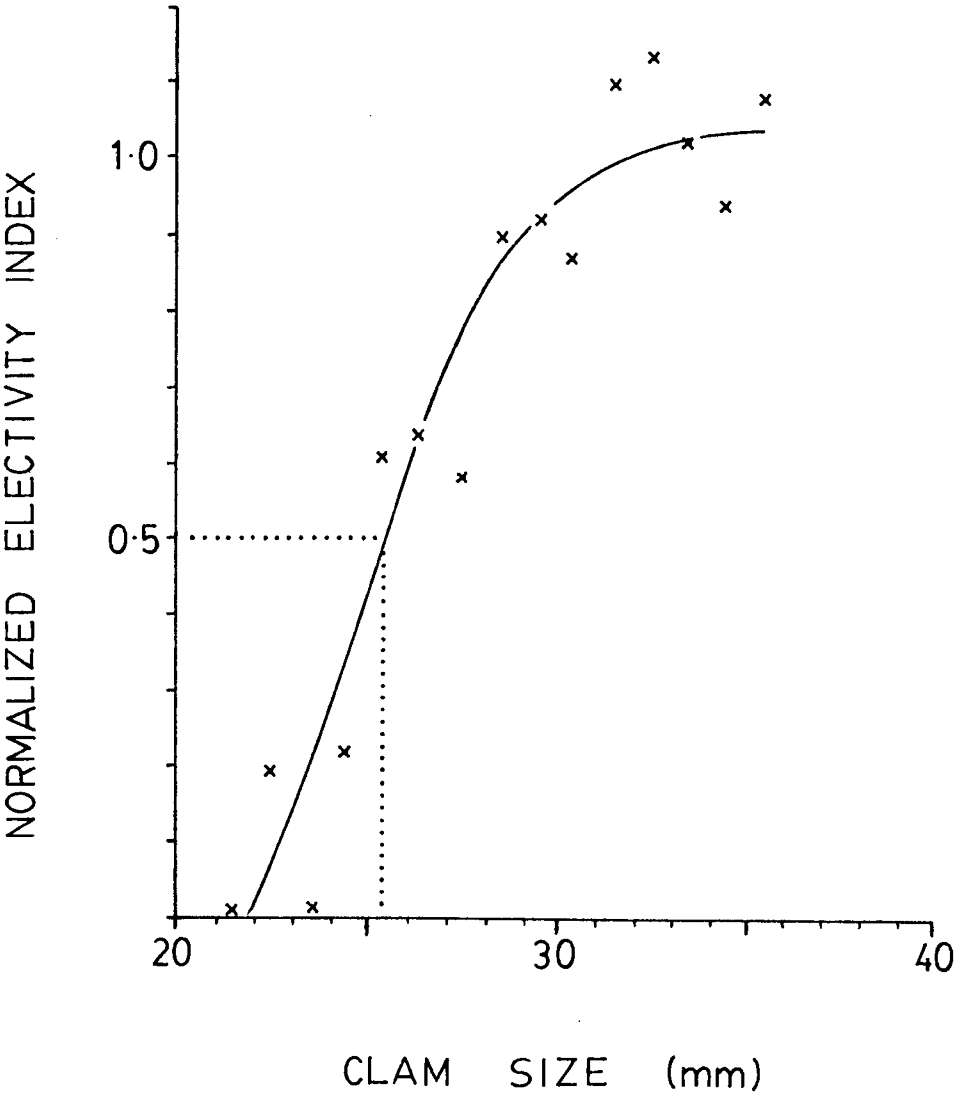


Fig. 29. Normalized electivity indices of yearling crows for each size class of littleneck clam. The level of 50% preference, assumed to represent the average yearling's choice of diet, is shown at 25.5 mm.

Table 18. Mean duration in seconds of search and handling times of adult and yearling northwestern crows feeding on littleneck clams in Well Bay. Sample sizes are given in brackets.

Activity	Time	
	Adults	Yearlings
Searching	34.6 ± 4.09 (186)	64.4 ± 5.93 (70) ***
First drop	4.2 ± 0.64 (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)

*** $p < .001$, ** $p < .01$, * $p < .05$

significantly more than the 1.7 drops per clam required by adults (Mann-Whitney U test, $0.05 > P > 0.01$). A comparison of the frequency distribution of the numbers of drops made by adults and yearlings is shown in Fig. 30. The difference seems best explained by poor choice of substrate, and slower or less direct flight. Over the size range of clams eaten and the range of drop heights used, the number of drops made by yearlings to break a clam was independent of its size. Therefore this difference was not a result of the yearlings' increased diet range. A limited amount of data and subjective observation suggested that yearlings dropped clams from a greater height than adults (pers. obs.). The longer duration of flights to the first drop supports this observation, especially given the similarity in durations of return flights from the drop zones to the clam bed. The greater drop height used by yearlings is contrary to the observations of Barash _et al_. (1975) and Maron (1982) on immature gulls. However, unlike gulls, the crows lost few clams to kleptoparasites and this was probably only a minor influence in their choice of drop height.

In contrast to adults (Chap. VII), the time it took yearlings to extract the meat from broken shells (Fig. 31) was independent of shell size (Kruskal-Wallis test, $P > 0.9$). It is unlikely that extraction time would be constant over the whole range of sizes, especially those as small as 10 mm. However, changes in this relationship have little effect on the predicted optimal diet. This diet was calculated using (i) a constant (the

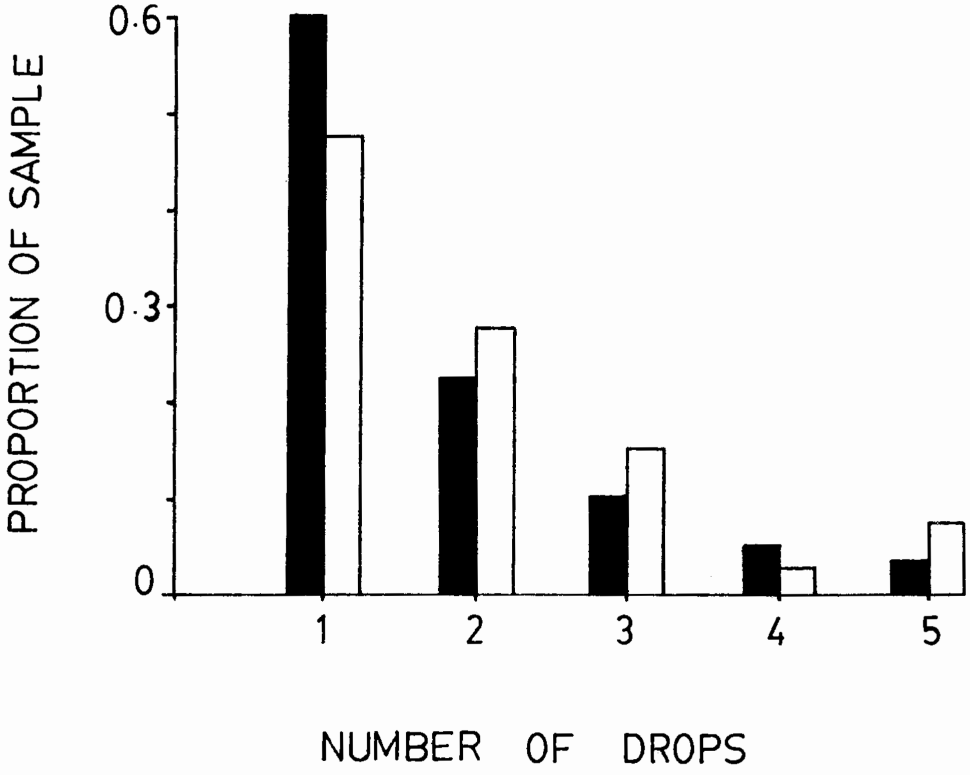


Fig. 30. Comparison of the frequency distributions of the number of drops required by yearling (open bars) and adult (solid bars) northwestern crows to break open littleneck clams. The distributions are based on the breaking of 153 and 460 clams, respectively.

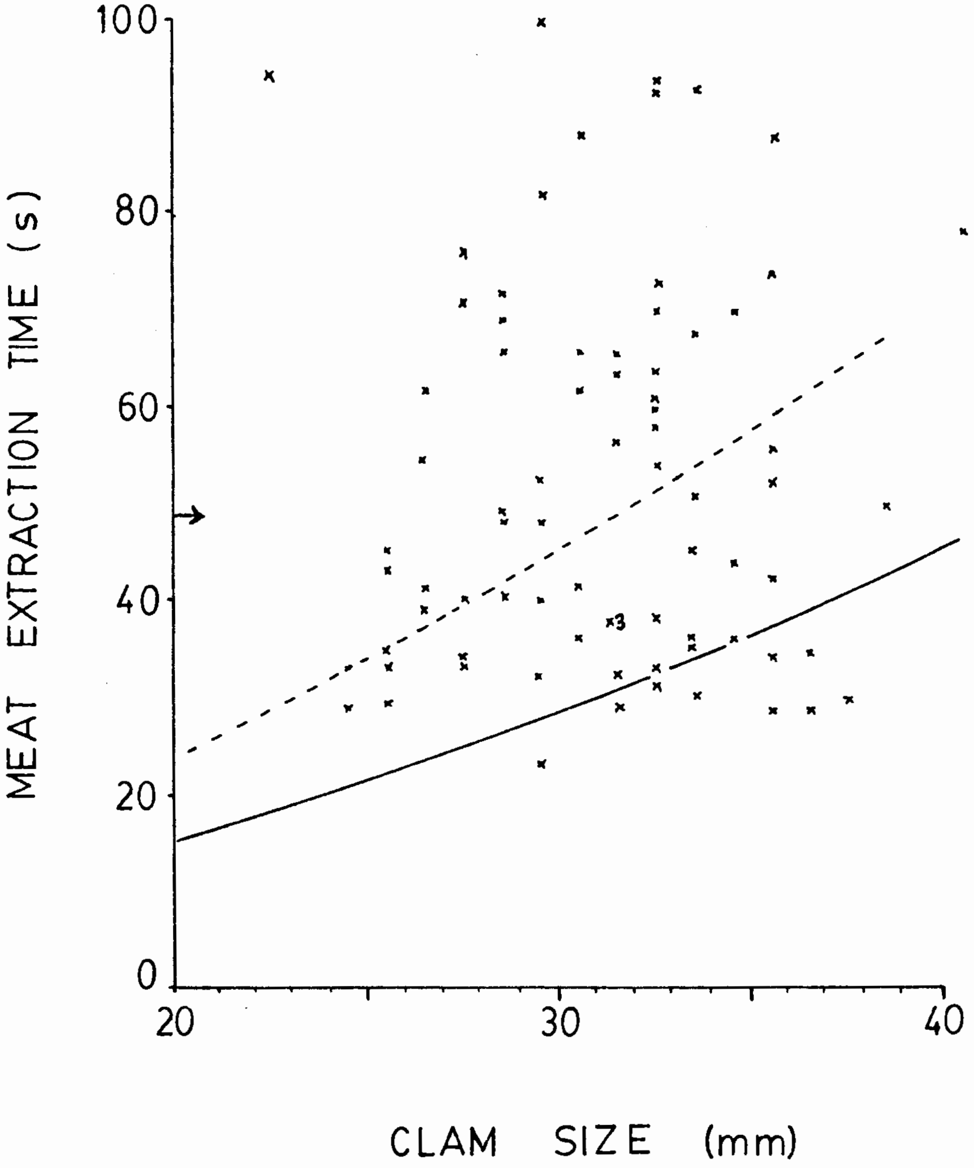


Fig. 31. The time for yearling crows to extract the meat from 76 littleneck clams ranging from 22 to 38 mm in length. The relationships between extraction time and size observed in adults (——) and a modified relationship used as an alternative (see text) to a constant extraction time for yearlings (----) are shown. The arrow indicates the median time for all observations.

median observed time) extraction time of 48.7 s (ii) a functional relationship between size and extraction time with the same exponent but with a small arbitrary increase in the y intercept observed for adults (Fig. 31). The predicted optimal diet was the same in both cases. Ranking of the prey, in terms of net energetic worth, was also unaffected by this relationship. As was the case for adults (Chap. VII), net energetic value increased with clam size.

The optimal diet

By sequentially adding smaller size classes to the theoretical diet, I calculated that the maximal net yield for a yearling would result from a diet containing clams of 25.0 mm or larger (Fig. 32). This is within standard errors of the observed lower limit to the diet of 25.5 mm. Such a diet would produce approximately 13 J/s, considerably less than the maximum of 47 J/s obtainable by an adult crow from its optimal diet.

DISCUSSION

There seems little doubt that yearling crows fed less efficiently on littleneck clams than did adults. This was true for every part of the foraging sequence measured, except the time to fly back to the beach (Table 18) and in the choice of the optimal size range of prey. Young common crows (*Corvus brachyrhynchos*) are close to adult weight when they fledge (Emlen 1936, see also Chap. IX) and also appear to achieve

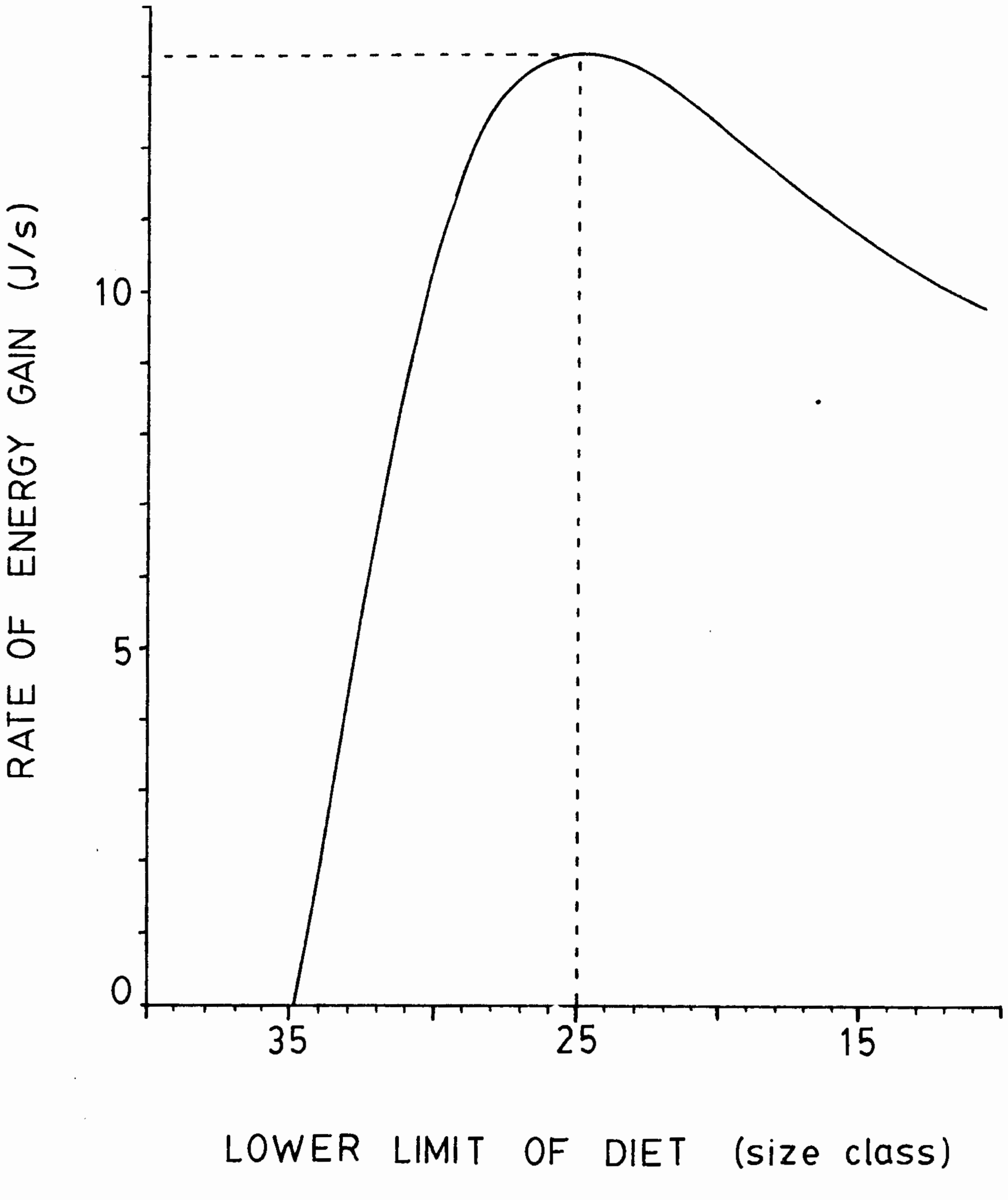


Fig. 32. The expected net rate of energy gain for a yearling crow from all possible diet breadths. The maximal gain is obtained from a diet of clams 25.0 mm or larger and yields just over 13 J/s.

flight capabilities approaching those of adults within a few months of fledging. Consequently, as with other young birds (Barash _et al_. 1975, Moran 1982), it is unlikely that the source of this juvenile inefficiency is maturational.

Skill learning

Young crows may be dependent on their parents for many months, with a few yearlings remaining associated with their parents into the following breeding season as helpers at the nest (Verbeek and Butler, 1981). While dependent, the young follow their parents closely, frequently standing almost in contact with the adults, and cocking their heads, seemingly to better observe their parents′ activities. Consequently, improvements in the performance of complex skills probably result from both observation and imitation of the activities of parents and through trial and error.

Despite this prolonged contact, young birds still required a considerable amount of trial and error experience to achieve a reasonable level of proficiency. I saw one yearling crow make a series of drop flights in which it failed to release the clam. Another dropped clams from a standing position, sometimes as many as 25 times, before either abandoning them or resorting to flying drops. Others experimented with dropping two clams simultaneously. In 4 y of observation one adult was seen doing this regularly and one other tried it on a single occasion. Although considerably more adults than yearlings fed on clams, three yearlings were frequently observed attempting to drop two clams at a time. For them this represented a maximum possible saving of 4.9 s per clam (the average of 6.1 s per first drop and 3.7 s per return flight) or 32.4 J. This is about 4% of the total energy expended in finding and handling a clam and is offset by two sources of loss. The birds experienced difficulty in (i) manouvering the shells so both could be grasped and (ii) locating both clams after dropping them. Consequently, dropping two clams at once is probably not energetically expedient for yearlings, but for the one adult that did so consistently, it appeared to be advantageous. In addition to the saving on time spent in flight, both clams were frequently extracted from the same hole and losses after dropping were rare.

If dropping clams two at a time can be advantageous why do more adults not do it? Shell dropping has been observed in rooks *Corvus frugilegus* (Priestley 1947), common crows (Goodwin 1976), hooded crows *C. corone* (Tinbergen 1953), white-necked ravens *C. albicolis* (Meinertzhagen 1959) and the northwestern crow. The ubiquity of shell dropping among crows makes it unlikely that dropping two together is a novel behavior spreading into the population. Consequently, it is possible that some of the young may experiment with this behavior but abandon it before becoming adults. Behavioral plasticity is probably vital for the young of animals that employ complex foraging strategies such as prey dropping. Different prey types may require different tactical approaches. For example, crows on Mitlenatch usually dropped clams from a height of less than 1.5 m, while on Mandarte Island, British Columbia, they dropped whelks (Thais lamellosa), with their more robust shells, from an average height of 5 m (Zach 1978). If the adoption of one set of tactics diminishes the ability to learn another set (Olive 1982), yearling crows feeding on clams may be faced by an interesting choice: to persist in trying to perfect a technique for dropping two clams at once and gaining a long term advantage or to opt for the easier task of dropping one at a time and the short term advantage. The rare use of this tactic by adults suggests that as young birds they opted for the short term gains.

Diet selection

The one aspect of foraging in which the young apparently do achieve the same level of performance as adults is in selecting a diet which maximizes, within the constraints of some obvious inefficiencies, their net rate of energy intake. My a priori assumption was that the seemingly greater sophistication required to make such a choice would be slower to develop than learning the relatively invariant optima of drop height, meat extraction methods and other purely mechanical processes involved in handling the clams. Two possibilities should be considered. Firstly, the agreement between observed and predicted diet limits may not be as good as the data suggest. Both the potential inaccuracies in calculating the lower limit of the yearlings' diet and a presumed higher degree of individual variability in the performance of the tasks involved, introduce a higher error margin compared to the adults. Secondly, the agreement between observed and predicted diet limits for yearlings was perhaps a fortuitous accident rather than the result of selective feeding. Diet selection by young birds was largely directed by their parents, who initially cracked open clams and left them for the attendant young to remove the meat. Subsequently, they simply dug up clams and placed them in front of the young who were left to break the clams themselves. At this stage, while still learning to dig for prey, the young also found and ate smaller clams that other birds had rejected. This mixture of clams, intentionally and unintentionally presented to them, was very similar to the size range which they took as independent yearlings. For these reasons it was impossible to establish conclusively, the extent to which the young themselves, or their parents, were actively selecting the size range of clams which the young ate and which produced the maximal energy gain.

The need to optimize

Sih (1982) stressed the importance of selection pressure in forcing predators to find solutions to foraging problems which are optimal rather than merely better than random. Crows do not start breeding until their second spring or later and from observations on 3 marked birds breeding for the first time, even these attempts may be singularly unsuccessful (James 1979). The occurrence of delayed and co-operative breeding, as exhibited by these birds (Verbeek and Butler 1981), has been attributed to strong competition for mates and nesting sites (Brown 1974,1978). If the chance to breed were limited, for young which were already at full adult size and weight, the selective value of foraging optimally may have been low. For a yearling crow, obtaining a possible maximum net energy gain of 13 J/s, or approximately twice its standard metabolic rate, 8 h of continuous clam foraging will just provide it with sufficient energy to spend the remainder of the day at rest. Unfortunately, with the limited amount of data available, it is impossible to determine whether the young take their time while foraging because there is little reason for them to hurry, or whether they delay breeding because they are unable to gather food quickly enough to raise young. In either case, the apparent selection of a diet which maximizes energy intake rate seems anomalous in the yearlings which generally show a low level of skill in their foraging technique.

IX. THE IMPORTANCE OF CLAMS TO BREEDING CROWS

INTRODUCTION

The ultimate aim of any ecological study must be to enhance the overall understanding of the functioning of biotic communities. Laboratory studies of basic ecological principles such as diet selection may provide valuable insight into the decision making processes of animals, but results from these studies have limited applicability in understanding the daily activities of a particular species in its natural habitat. The power of field studies in integrating the theoretical concepts of optimal foraging theory and the general biology of a local population is exemplified by the work of Tinbergen (1981) with starlings (Sturnus vulgaris), and that of Werner and Hall (1974,1979), Mittelbach (1981) and Werner, Mittelbach and Hall (1981) with bluegill sunfish (Lepomis macrochirus).

I have shown (Chap. VII) that northwestern crows feeding on littleneck clams on Mitlenatch Island can achieve a maximal net energy intake rate of 47 J/s. However, this value is only obtainable while the bird forages actively for clams and ignores both the need to perform other activities and the utilization of other potential food sources. In this chapter I attempt to assess the daily and seasonal use of various food sources. The probable rate of energy gain from foraging in different areas is estimated and related to the birds' utilization of those areas. The estimated daily energy gain from the observed pattern of use of the various food sources, and from feeding on clams alone, is compared with estimates of the birds' daily energy expenditure on other activities, particularly reproduction. The crows on Mitlenatch lay an average of 4 eggs per clutch (Richardson, Verbeek and Butler. MS.). Hatching success, close to 80%, is similar to that of many other passerine species (Lack, 1954). However, only about 30% of the nestlings survive to fledge, and this poor fledging success is amongst the lowest for passerines (Lack 1954). The majority of these deaths occur within 7 d of hatching and apparently are due mostly to starvation (Richardson, Verbeek and Butler MS.). This chapter considers whether these observations are consistent with the estimated energy available to the parent crows.

METHODS

The data were gathered on Mitlenatch Island, British Columbia, during the springs and summers of 1979 to 1982. All tide heights are heights above chart datum, which is defined by the Canadian Hydrographic Service as the level below which few tides drop (Anon 1983). The intertidal area of Camp Bay (Map 2) offers 2 main sources of food: (i) clams from beds located between 2.4 and 3.3 m and (ii) a variety of organisms found in extensive Ulva beds. The latter are mainly below the 1.5 m tide level, with the exception of one small tongue of seaweed extending up along the rocky shore on the west end of F Island to about the 2 m level. As the spring and summer progress, the weed is exposed to the heat of the sun for increasing lengths of time and the actual cover decreases from a high of 100% in April to an estimated 50% by late July.

Throughout May, June and July of 1980 and 1982, between sunrise and sunset on approximately every third day, I made hourly counts of the number of crows feeding in each of these 2 areas. On the same day I also collected newly broken clam shells from the drop zones just before they were covered by the incoming tide (see Chap. V).

To estimate the amount of food available in the *Ulva* beds I sampled a total of eight 1 m randomly located quadrats. Each quadrat was sampled shortly after the selected area was uncovered by the tide, as crows prefer to forage close to the water's edge (Butler 1980). I placed all the *Ulva*, stones, shells and any visible potential prey items from each quadrat into a bowl. This material was then sorted to isolate the prey items. These were identified and their total wet weight measured on a triple beam balance. The number and type of prey captured by crows foraging in the *Ulva* over a fixed time period was recorded. Caloric content of each of the prey types was obtained from Cummins and Wuycheck(1971) and Thayer *et al*. (1973).

Details of the daily and seasonal activities of the crows on Mitlenatch Island, were obtained from Butler (1980) and James (1979), and of the breeding biology from Butler (1980), James

(1979), Verbeek and Butler (1981) and Richardson, Verbeek and Butler (MS). The energetic costs of activities were taken from Zach (1979) and references therein.

The energy demands for raising broods of different sizes were calculated by a similar method to that used by Ricklefs (1974) for the growth and maintenance of starling chicks. Growth data were fitted to a logistic equation (Ricklefs 1967) giving an asymptotic weight (W) of 310 g and a rate constant (K) of 0.285. The age dependent energy density of chicks (J/g wet weight) was calculated from the average of the intercepts and slopes of the equations given by Ricklefs (1974) for altricial species. The age specific basal metabolic rate was estimated by scaling the functional relationship between percent growth and metabolic rate for starling chicks (Ricklefs 1974) to Aschoff and Pohl's (1970) prediction of basal metabolic rate for the growing crow chicks. The costs of metabolism for broods of different sizes was calculated from the combined weight of all the chicks in the brood (Mertens 1969, Royama 1969). An energy conversion efficiency of 70% was assumed and the cost of movement and thermoregulation taken as 33% of the metabolic cost of maintenance (Dunn 1973, quoted in Ricklefs 1974).

RESULTS

Availability of clam and *Ulva* beds

The tidal cycle on Mitlenatch Island is of a mixed diurnal type. This results in a complicated annual exposure pattern for the clam and *Ulva* beds (Fig. 33). The main factors contributing to this pattern are;

1. the monthly spring high tides occur at night during the summer and in the day during winter,
2. during the summer months, the lower of the two daily high tides may be less than 3.5 m. When this happens, at least part of the clam beds is uncovered for almost 12 h.
3. during the winter months, the higher of the two daily low tides may exceed 3.5 m and the clam beds are covered for almost all the daylight hours.

In December 1982 the clam beds were exposed for a monthly average of only 10 min/d. The peak exposure, an average of over 12 daylight h/d, occurred in June (Fig. 34).

The *Ulva* beds, located lower in the intertidal than the clam beds, were obviously exposed for even less time. The tide rarely dropped below 1.5 m between early September and late March. The peak daily average exposure of 3.2 h/d occurred in July (Fig. 34).

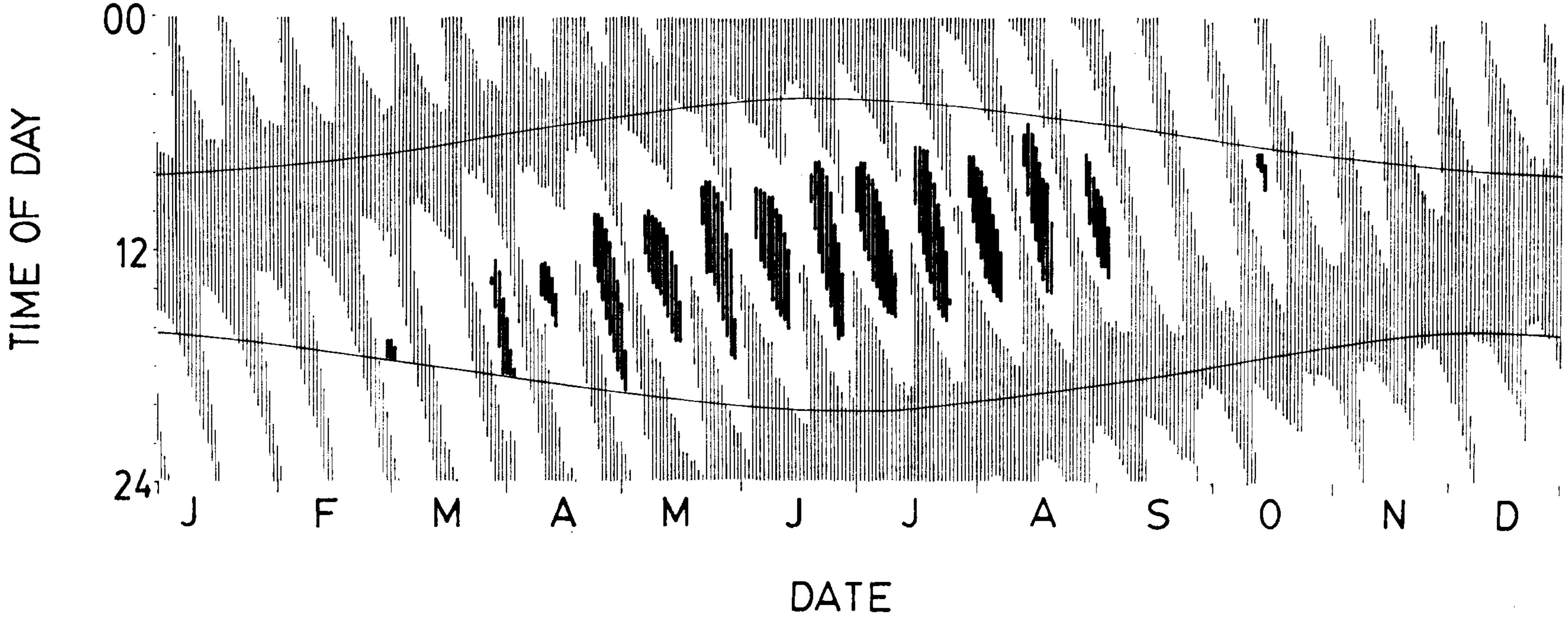


Fig. 33. Exposure, by the tide, of clam and _Ulva_ beds on each day in 1982. Narrow vertical lines show the times when the tide is higher than 3 m and the clam beds are covered. Thick vertical lines indicate the times when the _Ulva_ beds are uncovered (tides less than 1.5 m). Continuous curved lines show the times of sunrise and sunset.

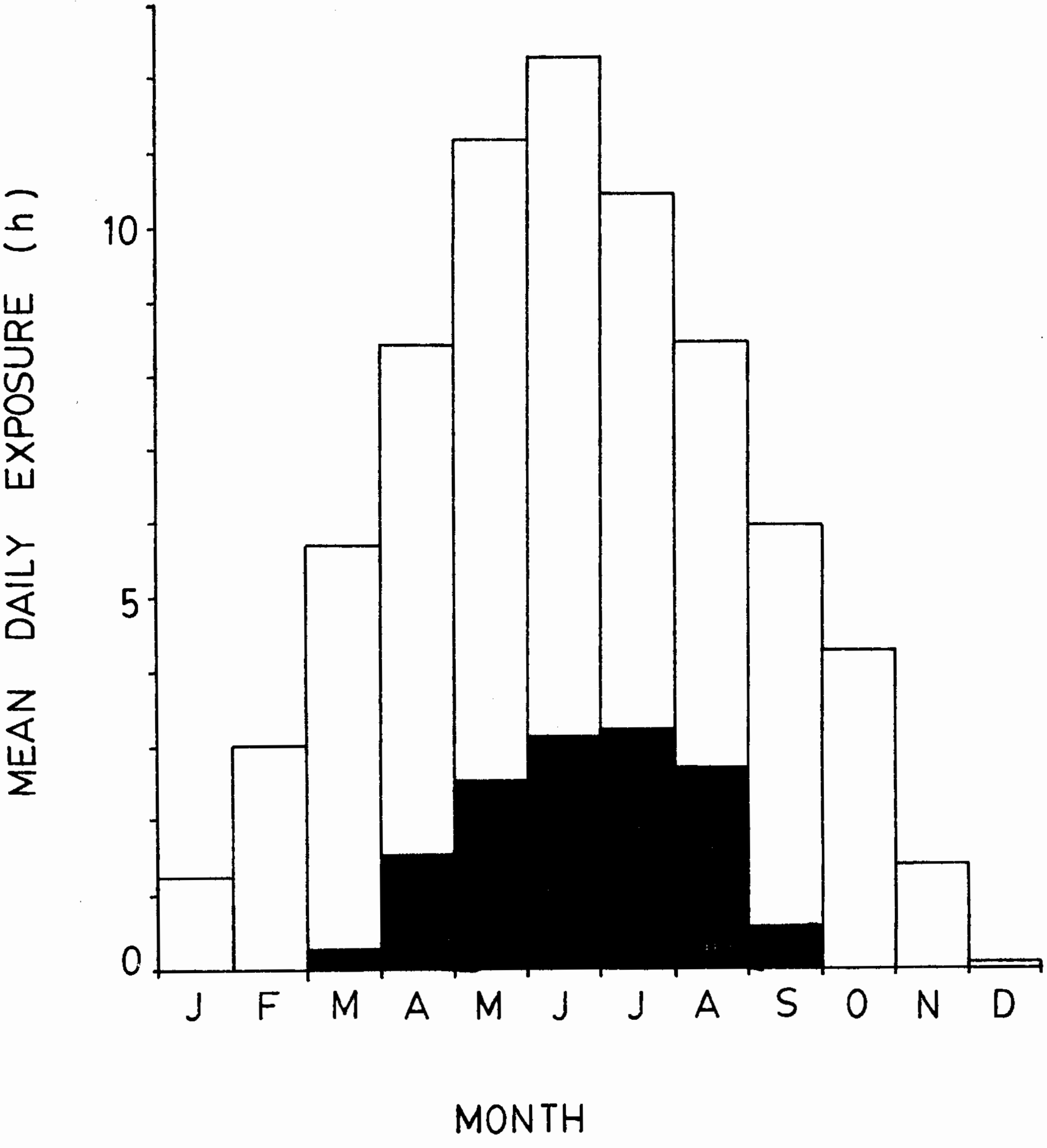


Fig. 34. The average number of hours per day during which the *Ulva* beds (solid portion of the bars) and clam beds (total of solid and open portions) were exposed by the tide in each month of 1982.

Utilization of clam and *Ulva* beds by the crows

The greatest use of the clam beds was at tide heights of between 2 and 3 m, while few crows fed there at tide heights of less than 1 m when the *Ulva* beds were uncovered (Fig. 35). Fewer crows per observation fed in the clam beds in May than in June, and there were fewer birds per count in July than in either May or June (Wilcoxon signed-rank tests, $0.05 > P > 0.01$, $0.05 > P > 0.01$ and $P < 0.005$ respectively).

By comparison, the greatest utilization of the *Ulva* beds was at tide heights of 0.3 to 1.3 m (Fig. 36). The average number per observation decreased over successive months (Wilcoxon signed rank tests, $P < 0.001$ in both cases). The maximum number of crows feeding in the *Ulva* beds was greater than the maximum observed feeding in the clam beds at any time.

The number of clams eaten per day varied greatly (Fig. 6). In general, the fewest clams were taken on days when the *Ulva* beds were exposed for a long time and vice versa. This is consistent with the observation that during low tides, the crows fed preferentially in the *Ulva* beds.

Energy gain from clam and *Ulva* beds

The total wet weight of potential prey items in the *Ulva* quadrats (N = 8) ranged from 3.5 to 18.5 g. An average 81.5% (range of 62.2 to 85.4) of this weight was polychaete worms.

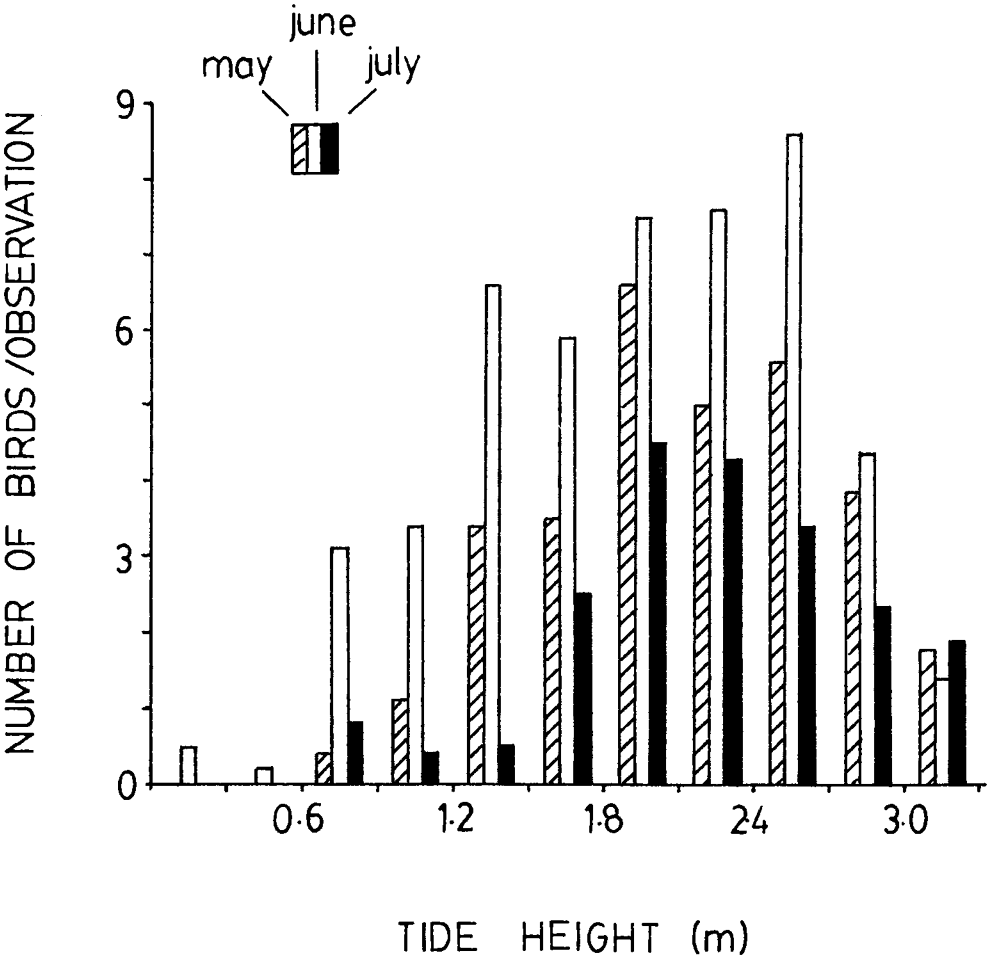


Fig. 35. The average number of crows observed foraging in the clam beds at different tide heights. The counts were made at hourly intervals, on approximately every third day, during May, June and July of 1980 and 1982.

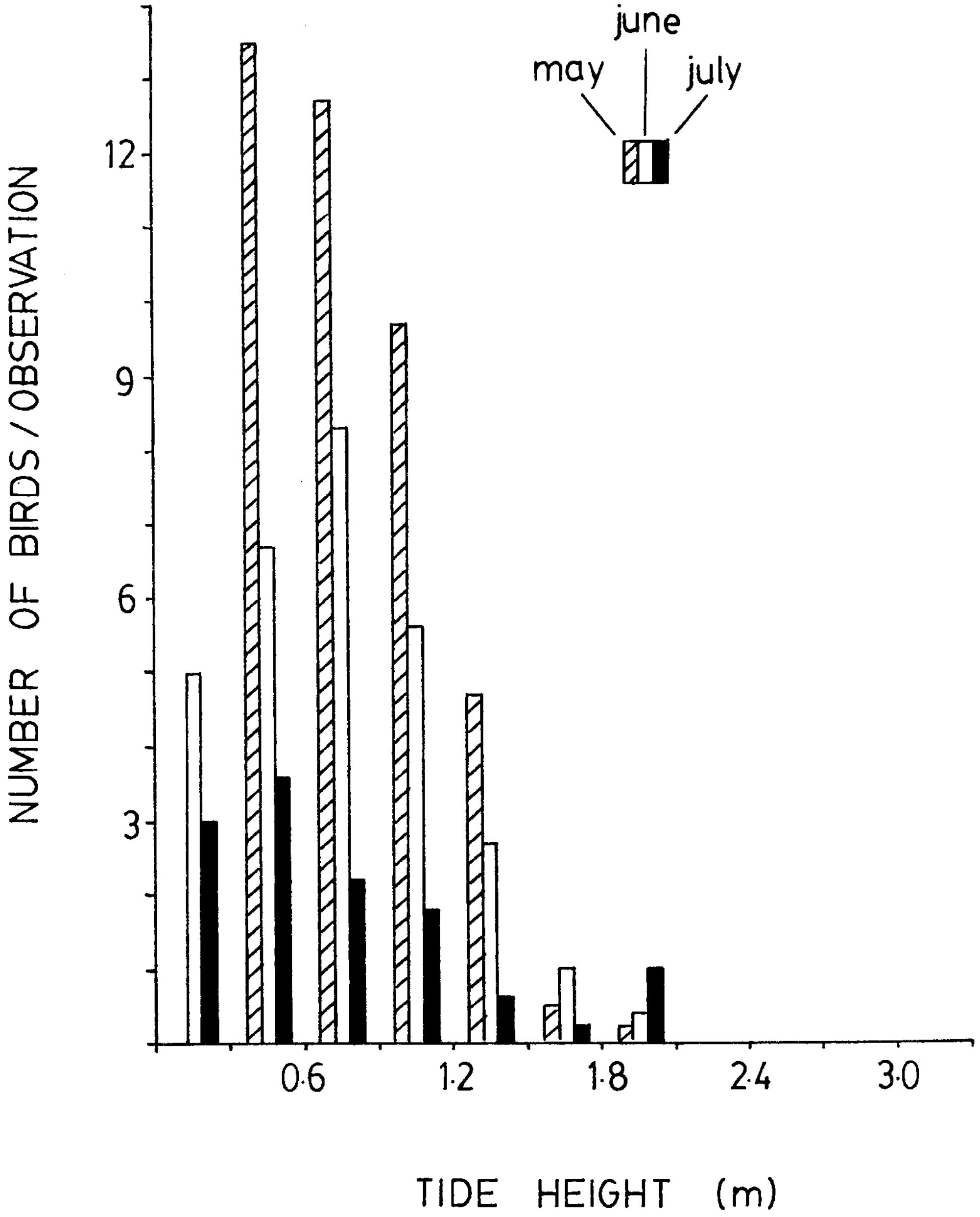


Fig. 36. The average number of crows observed foraging in the Ulva beds at different tide heights. The data were collected in the same way as those for Fig. 35.

The remainder was composed mainly of nemertine worms, caprellid and gammarid amphipods, shore crabs (_Hemigrapsus_ _nudus_ and _H._ _oregonensis_) and kelp craps (_Pugettia_ _gracilis_). The crows were seen to capture red rock crabs (_Cancer_ _magister_) up to 15 cm across the carapace, polychaetes of up to 15 cm and small (about 7 cm), eel-like fish, probably of the families Ptilichthyidae, Pholidae or Blennidae. None of these larger items were encountered in the samples.

In 92 min of observing individual crows foraging in the _Ulva_ beds, I saw them capture 256 items: 132 assorted worms, 20 gammarids, 7 crabs small enough to be swallowed whole once the legs had been removed, 4 fish and 93 unidentified small organisms. This is an average of 86 worms/h and 160 food items/h. Butler (1980) recorded a capture rate of 65 items/h. This discrepancy is probably due to the variability of the _Ulva_ cover, which is influenced by such environmental factors as wind strength and direction and the temperature at low tide. From the combined weight of 148 nereids, the average weight per worm was calculated as 55 mg. The mean of three caloric values for nereids given by Cummins and Wuycheck (1971) and Thayer _et_ _al_. (1973) is 3990 J/g wet weight. This provides the crows with 18.9 kJ/h from eating worms. I assumed that, with the exception of the fish, the crows took food items in roughly the same weight ratio as they appeared in the samples. The similarity in numbers of prey types between the samples and the diet suggest that this is not unreasonable. I further assumed that the other prey types in the Ulva beds had similar caloric values. Hence, the energy gained from all prey in the Ulva beds, except the fish, was 18.9/.815 or 23.2 kJ/h. Thayer et al. (1973) gave an average caloric content of 5.04 kJ/g wet weight for 23 species of bony fish. Using a generous weight estimate for a 7 cm blenny like fish of 4 g, 4 fish every 92 min produces 52.6 kJ/h. With an assimilation efficiency of 70%, the total gain from the Ulva beds was 53.1 kJ/h ((52.6 + 23.2) x .7). Subtracting an energetic cost for search and handling of three times the basal metabolic rate (Zach 1979 and references therein) reduces this to a mere 14.0 kJ/h. This falls far short of the theoretical maximum of 169.2 kJ/h (47.0 J/s x 3600 s) from feeding only on clams.

The number of hours during which the birds can feed is limited by the availability of foraging areas and the need to satisfy other demands. In June, when most nestling growth occurs (Butler 1980), there were approximately 16 h daylight/d, during which the clam beds were exposed for 12 h and the Ulva for only 3 h. Crows only forage for about 72% of the daylight hours (James 1979), with most of the remainder spent resting and preening. These latter activities are concentrated in the early morning and pre-roosting hours (pers. obs.) even when the intertidal is uncovered at these times. During the middle of the day the birds appear to forage continuously, except for flights to feed the young and drink. Since the young are fed only about three times/h and adults drink from pools close to the drop areas this is not a major energy expenditure for those birds that nest close to the beach. However, these birds do have greater success in rearing young from hatching to fledging than birds which nest in the interior of the island (Verbeek and Butler 1981), suggesting that travel time from the feeding area to the nest can be a significant factor in a bird's energy budget. Of the time spent foraging about 60% was spent in the intertidal. With an average of 4 h/d (25% of the daylight) when the intertidal is covered by the tide, the birds must spend at least 15% of the day foraging preferentially in other areas.

Given that the clam beds offered the best rate of energy reward to a foraging crow, I calculated the upper limit to their expected energy gain as the energy gained by feeding for 12 h on clams and spending the other 12 h at rest. The net gain while foraging would be 2030 kJ/d, minus the metabolic cost of 304.5 kJ/d (twice the basal metabolic rate) while at rest, giving a surplus of 1726 kJ/d for use in reproduction.

Energy demand of growing chicks

The maximal demand for biosynthesis of 168 kJ/d per chick, occurred at the mid-point of growth (Fig. 37). Because the basal metabolic rate of chicks rises above the adult level, the cost of maintenance also reaches a peak in mid-development (Fig. 37). The combination of growth and maintenance results in a maximum daily requirement per chick of 533 kJ/d. This figure seems in accordance with the 105 kJ/d for a 70 g starling calculated by

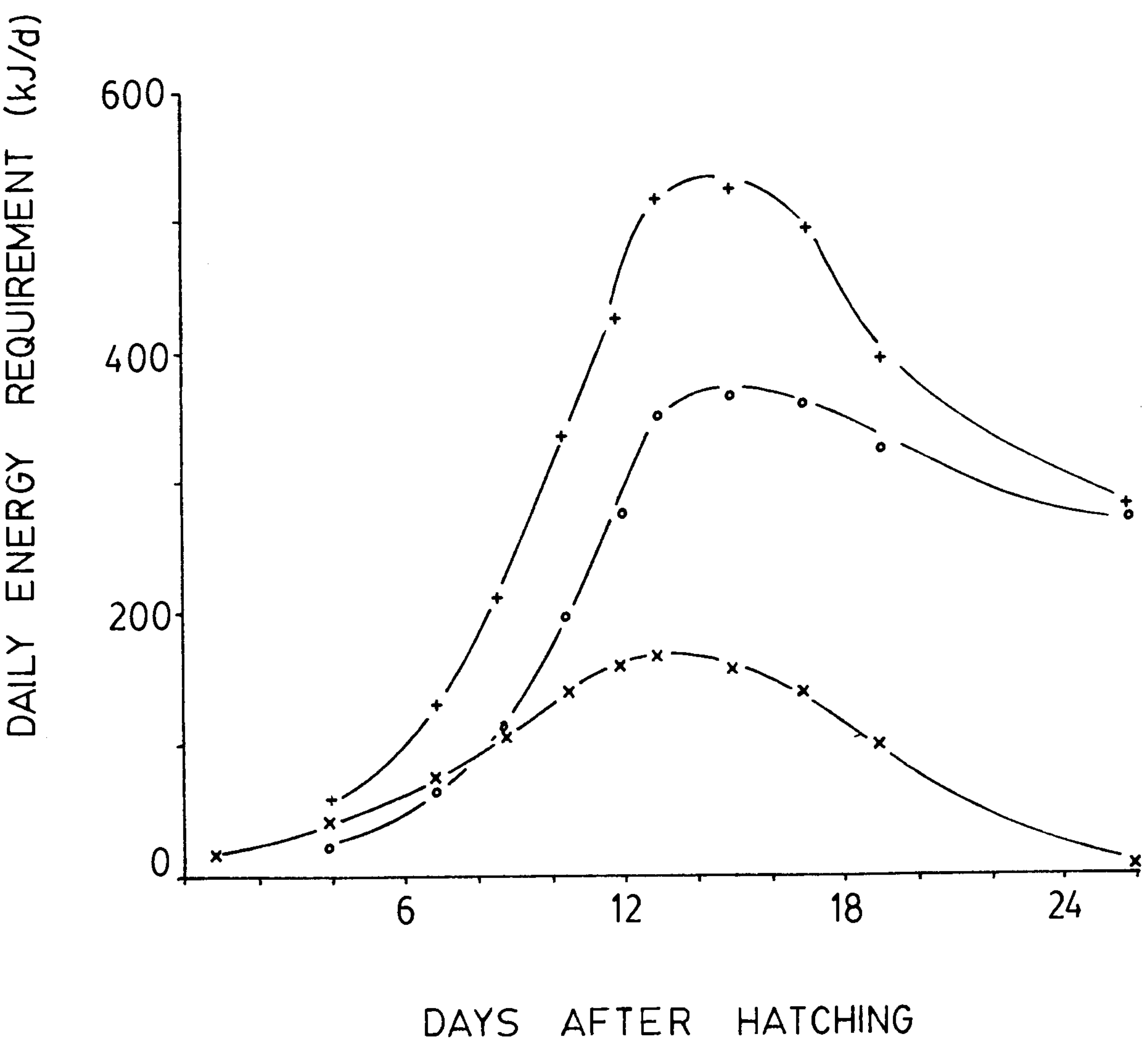


Fig. 37. Estimated daily energy demands for biosynthesis (x-x), maintenance (o-o) and total daily energy need (biosynthesis plus maintenance, +-+) to raise a crow chick. Details of the computation of these energy requirements are given in the text.

Ricklefs (1974) and which excludes the costs of thermoregulation and movement. It is also similar to the 650 kJ/d calculated by Yom-Tov (1974) using a different method, for a 500 g carrion crow chick. The maximum daily requirements for broods of 1,2,3 and 4 chicks were estimated at 533, 928, 1280 and 1615 kJ/d, respectively.

DISCUSSION

The data presented in Chapter VII provided very strong evidence that the crows on Mitlenatch Island do maximize their net rate of energy intake while feeding on clams. However, the data presented in this chapter, concerning their utilization of other food sources, are inconsistent with an optimization model based only on the maximization of net energy intake. Although a number of estimates were incorporated in the calculation of profitability of the *Ulva* beds, the almost 10 fold difference in the predicted gains from clam and *Ulva* beds, makes it unlikely that the difference is not real. Despite this, the crows on Mitlenatch incur an energetic loss by preferentially foraging in the *Ulva* beds. Goss-Custard (1977a) reported a similar energetically inappropriate choice by redshank (*Tringa totanus*) when feeding on *Corophium* and polychaete worms. He suggested (Goss-Custard 1981) a number of possible explanations for this apparently aberrant behavior.

Firstly, it may be harder to assess and rank the profitability of different prey species, than different size classes of a single species. However, since crows appear to maximize energy intake while feeding on clams (Chap. VII), they must have some relatively sensitive method of measuring their intake (Dill 1983, Ollason 1980). Changing their diet in response to manipulations of search and handling costs indicate that the crows do possess such a mechanism and should consequently be aware of the low energy gain from feeding in the *Ulva*.

Secondly, the *Ulva* may have been, over the course of time, the more reliable resource. The Japanese littleneck clam is a recent introduction to British Columbia (Neave 1944), prior to which the *Ulva* beds may have presented the most profitable foraging on the island. However, unlike the redshank with its limited foraging repertoire, there must be little advantage to such an opportunistic feeder as the crow, to develop any strong reliance on a single prey species or foraging area.

Lastly, the selection of food types may be dictated by the need to optimize some dietary component other then energy. The rough calculations of the energetics of raising young crows suggests that a crow should be able to raise four young if it fed only on clams. This would be so even if the bulk of the brooding female's energy needs must be provided by the male. Her nest attentiveness drops from 90% to as low as 40% at about the 10 th day after hatching (Butler 1980), which is well before the broods' peak demand. Nevertheless, 51% (86 of 169) of the chicks died within 7 d of hatching, at a time when the total energy need for the brood is still less than the daily maximum for a single chick. Also chick mortality is independent of brood size (Richardson, Verbeek and Butler. MS.). The frequent occurrence of shellfish poisoning in British Columbia waters (Quayle 1966), may put a serious constraint on the extent to which shellfish can be used as an energy source. On Mitlenatch, the crows should be able to catch as many as 40 clams/h, yet observation of individual birds and the daily total consumption by all the crow using the beach, showed that such a pace was never achieved. At that rate the clam population would be depleted rapidly. Since the clam beds were not exclusively defended, the alternative to limited clam consumption being the result of simultaneous optimization of energy and some other nutrient factor, is the currently untenable theory of group selection.

X. A FINAL COMMENT

In this thesis I have described the foraging behavior of northwestern crows and tried to determine if this behaviour is consistent with the hypothesis that animals maximize their net energy intake rate. Much research in optimal foraging has provided qualitative support for this hypothesis (see Krebs *et al*. 1983 for a comprehensive review). This repeated partial success has encouraged refinement of the original models to incorporate additional constraints. However a general reappraisal of the methods of ecological research (Strong 1980,1983, Connell 1983, Quinn and Dunham 1983, Roughgarden 1983, Simberloff 1983, Gould and Lewontin 1979, Lewontin 1979) have led to the condemnation of optimal foraging theory as unscientific (Lewontin 1979, Gould and Lewontin 1979).

Simberloff (1983) acknowledges that "the search for confirmatory evidence is easier than the search for falsification and is very seductive" but advocates strict adherence to the falsificationist approach proposed by Popper (1959) and Platt (1964). Defenders of optimal foraging theory say that proof of optimization is not their aim, only the establishment of a set of predictive rules for foraging behaviour (Smith 1978, Krebs *et al*. 1983). Alternatively, they suggest that overlapping and interactive factors in complex ecological situations make it impossible to formulate mutually exclusive, alternative hypotheses (Quinn and Dunham 1983).

Since it is unlikely that all animals follow the same set of rules in selecting varied prey from a multitude of different habitats, I agree with the proponents of optimal foraging theory in suggesting that searching for a provable hypothesis is counter-productive. Consequently, although the research reported here may approach a philosophically intractable problem, I feel it has made important contributions to producing a set of generally applicable foraging rules which will be of use to field ecologists in predicting feeding behavior.

1. It provides one of the most conclusive field demonstrations of selective feeding yet published. The argument for selectivity is particularly strong because there is an inclusion of the predators' searching tactics in the determination of prey availability (Chap. VI). Also, because there exists a size range of clams captured but rejected by the crows which is intermediate between the size ranges of those eaten and those never captured (Chap. VII).
2. The results provide a reaffirmation of energy maximization as a major determinant of diet selection and they provide further support for the general applicability of energy based models. The simple model used in my research twice provided quantitative agreement between observed and predicted diet limits (for adults in Chap. VII and yearlings in Chap. VIII) and twice gave qualitative support (for broken and unbroken clams taken from the feeding tables in Chap. VII). Agreement with the predicted directional changes

between tests strongly suggests that energy is an important factor in diet selection.

3. This is perhaps the only field study to make precise predictions of diet breadth rather than simply attempting to detect directional shifts in diet breadth with changing prey density (Goss-Custard 1977, Werner and Hall 1974). The methods used here should allow more accurate testing of refined models than would the methods of the above authors. The more accurate are the predictions of a model, the more restrictive will become the null hypothesis and therefore more powerful will be the tests of the model.

4. Finally, the failures of the model provide valuable information on the direction of future research. The inaccurate predictions of the minimum sized clams taken from the feeding tables suggests that crows are either unable to extrapolate to new situations, do not attempt to maximize their energy intake, or that the parameter values used in the calculations are wrong. The crows′ contradictory preference for feeding in the _Ulva_ beds indicates that they are using a different set of decision rules or are grossly errant in their energy assessments. More accurate measures of the parameters incorporated in the model may help in showing if crows simply do not maximize their energy intake rate. A greater understanding of the mechanisms used by the birds in assessing the value of a single clam or of the energy intake from a particular diet is needed. Such

information would help in establishing if there are any sensory constraints on the birds′ ability to perform optimally. A knowledge of the dietary and energetic requirements for both growth and maintenance may help establish which other factors, if any, should be considered in subsequent models. The affects of interspecific aggression and the demands of other non-foraging activities may also prove to be of major importance in the foraging process.

Though great strides have been made toward understanding feeding behavior it seems that further progress is dependent not only on the production and testing of more complex models, but on a better understanding of the total ecology of our research animals.

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