SOME ASPECTS OF FEEDING AND FORAGING
BEHAVIOUR OF THREE CORVIDS IN NEWFOUNDLAND

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Some Aspects of Feeding and Foraging Behaviour
of Three Corvids in Newfoundland

by

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Abstract

Research began with a study of nest predation by a pair of Common Ravens in a colony of cliff-nesting kittiwakes during summer, 1979. Patrols by single ravens were twice as successful as when both birds hunted together. Kittiwake anti-predator defense was important in reducing predation. Results of a cost/benefit analysis suggest that the ravens obtained sufficient prey to meet daily energy requirements.

A series of feeding and foraging experiments, designed to test several basic assumptions of Optimal Foraging Theory, was carried out between September 1979 and June 1980, using freeliving Gray Jays and Common Crows and artificial prey populations. Both species became more discriminating in bait selection when relative and absolute abundances of profitable baits were increased. When populations of artificial baits consisted of two and three different types, jays differentially selected bait types on the basis of net energy value. Individuals differed in food preference and foraging efficiency. The possible influences of social status and prior experience are discussed.

Three experiments were designed to induce switching of prey preferences among the jays by decreasing the profit-

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ability of a preferred food. Manipulations that produced increases in handling, search, and recognition times caused the jays to switch to an alternate bait, but they were reluctant to take a second alternate that was low in net energy value. Many of these data support current models of Optimal Foraging Theory.

In a final experiment, a Great Horned Owl decoy was used to disrupt the feeding behaviour of a family of Gray Jays. Differences were found between juveniles and adults in anti-predator behaviour and food preference, juveniles being less cautious in the presence of the decoy and less discriminating in bait preference. Possible reasons for these differences are discussed.

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GENERAL INTRODUCTION

"The idea that nature pursues economy in all her workings is
one of the oldest principles in theoretical science."
— R.R. Rosen (1967)

Optimal Foraging Theory (O.F.T.) embodies a group of
economic models that predict that, through the process of
natural selection, animals should feed in an efficient
manner to obtain maximum fitness (Schoener 1971; MacArthur
1972; Emlen 1973; Pianka 1974; Pyke, Pulliam and Charnov
1977). In a given population, the average and modal for-
aging behaviour should be close to that behaviour that
results in maximum fitness (Pyke et al. 1977).

The rewards of efficient foraging are great: more
time and energy may be devoted to other activities such
as reproduction, territorial defense and maintenance. By
obtaining adequate resources in the least amount of time,
an animal gains a high 'foraging fitness' (Utter 1971).
Greenlaw (1969) has shown that Rufous-sided Towhees
(Pipilo erythophthalmus) produce larger clutches and
invest more time in reproduction when they forage in
a rich habitat, and Swanberg (1951) reports larger clutch
sizes in Clark's Nutcrackers (Nucifraga columbiana) when
food stores are abundant.

Foraging behaviour is shaped by four major factors

(Schoener 1971): i) food choice (optimal diet), ii) optimal allocation of time for feeding, iii) choice of food patch type, and iv) optimal movement patterns and rates of foraging. The nature of the optimal diet is assumed to be affected by three factors (Schoener 1971): i) the decision to eat low value foods depends solely on the abundance of high value foods, ii) an abundance of high value foods will lead to diet specialization since foods of lesser value will be dropped from the diet, iii) a particular food type should be eaten whenever it is encountered or not at all. That is, predators should not show partial preferences.

Models can be used to show exceptions to predictions and to determine reasons for such discrepancies. A common assumption of many optimal foraging models is that the 'currency' (Schoener 1971) to be maximized is energy. Different foraging strategies may in fact tend to maximize nutrient intake (i.e. an essential vitamin or amino acid), net rate of energy intake over a longer period such as a season or lifetime, etc. (Pearson 1974). Gathering of excess foods for caching, or energetic requirements of reproduction, may also influence foraging behaviour.

In the simplest analysis of optimal diet, one examines

the relationship between energy gain (E) and foraging time (T). Time for pursuit, handling and recognition of prey may be involved, depending on specific foraging demands and methods. If an animal with a net rate of energy intake (E/T) encounters a food item which yields energy, e, at a cost of time, t, that item should be eaten if the relationship $E+e/T+t > E/T$ holds. When this inequality does not hold, that food should be ignored (Cody 1974). Because values of E and T change over time and with prey availability, the inclusion of prey in the optimal diet will also change.

While many of the assumptions on which theoretical models are based, and many of the predictions they generate need to be validated in nature, data generally support predictions of existing models; however, inconsistencies have been found (e.g. Emlen and Emlen 1975; Goss-Custard 1976). In one test of O.F.T., Zach (1978) applied a cost/benefit analysis to the whelk dropping behaviour of Northwestern Crows (Corvus caurinus). For this type of analysis, knowledge of the animal's basal metabolic rate (BMR) is essential. BMR, defined as the minimal heat production in a fasting, resting animal (Kleiber 1961), is multiplied by caloric requirements of, and amount of time spent in, each activity

to yield an overall energy budget. Crows in Zach's (1978) study selected only large whelks from the intertidal zone and did not switch to medium- or small-sized prey when the preferred size was scarce. All size classes had an equal probability of breaking, but small and medium whelks contained too little energy to have been profitable for the crows. Zach determined the optimal height for shell break-age and found that the crows rose to the minimum altitude required to shatter whelks. This is an important con-sideration because ascending flight is costly (Bernstein, Thomas and Schmidt-Nielsen 1973; Tucker 1973).

Early studies by Popham (1942), Lack and Owen (1955) and Holling (1959) focused on the relationship between prey density and selection. Since Ivlev's (1961) finding of increased selectivity with an increase in food abundance, major interest has been focused on this problem. Evidence by Ward (1965) from weaverbirds (Ploceus spp.), Orians (1966) with blackbirds (Icteridae), Goss-Custard (1977a) with Redshank (Tringa totanus) and Krebs et al. (1977) with Great Tits (Parus major) all show increased selec-tivity by avian predators with increasing prey abundance. Similar findings by Werner and Hall (1974) from Bluegill Sunfish (Lepomis macrochirus) suggests a general principle

may be involved.

Prey density has also been shown to exert a large effect on foraging time, which in turn defines the optimal diet. An animal spends its foraging time searching for and handling prey. If only the best items are selected, a high rate of energy intake is gained, but more time must be spent searching. Non-selective predators spend little time searching but have a low rate of energy intake per handling time since their diets consist of high and low quality prey. If the encounter rate with profitable prey is low, the predator should be non-selective, but at high prey density low quality items should be ignored (Schoener 1971).

On the assumption that showing mixed preferences represents suboptimal foraging, models by Emlen (1966), Pearson (1974), Estabrook and Dunham (1976), Charnov (1976) and others predict that the probability of taking a particular prey type should be 0 or 1. This prediction of an all-or-none type of selectivity has been a shortcoming of O.F.T., as no researcher to date has found this type of functional response to increased prey density. Too often, normally occurring feeding responses such as switching (Murdoch 1969) and sampling (Krebs et al. 1977)

have been overlooked.

Switching from one prey type to another often results in a change in searching or foraging strategy (Murdoch 1969; Curio 1976), and may occur when a highly preferred prey decreases in profitability. If a predator must spend long periods of time searching for cryptic or scarce prey, less profitable prey may "move into" the optimal diet (Krebs et al. 1977). Switching may also reflect an animal's need to maintain a balanced diet, an effort to vary its intake, or simply mistaken selection (Pearson 1974). For whatever reason, switching is commonly observed in laboratory experiments as well as in the field.

Sampling has been viewed as sub-optimal foraging because it causes the animal to sacrifice a certain amount of efficiency (Krebs et al. 1977). However, when there are nutrient constraints on the diet, an efficient predator may still show mixed preferences. Pulliam (1975, p. 765) states: "It is obvious that a set of prey choices which maximizes caloric intake may or may not constitute a balanced diet for the predator." The common, and often mechanical assumption that energy is the currency to be maximized has been a limitation of many O.F.T. models.

Because O.F.T. experiments typically offer different sizes of a single prey type, differences in nutrient quality, palatability and energetic costs of handling have been ignored. Where these factors have been considered, it is apparent that animals can select profitable prey. Kear (1962) documented this in finches (Carpodacus spp.), as has Moss (1968) for Rock Ptarmigan (Lagopus mutus). Similar evidence has also been found for non-avian predators (e.g. Smith 1970; Menge and Menge 1974), yet not all predators always choose profitable prey, and Emlen and Emlen (1975) feel that this 'poor fit' may be the result of weak selection pressure for an optimal choice strategy. When assessing food choice it should be borne in mind that 'value is a multivariate entity involving caloric uptake, amino acid composition, physiological state of the animal, etc.'(Emlen and Emlen 1975, p. 428).

The feeding strategies of individual conspecifics foraging in similar habitats may be different. Partridge (1976) tested eight Great Tits in four different artificial habitats and found much variability in choice of habitat and preferred food. Individuals favoured those habitats in which they demonstrated the highest efficiency, in

terms of energy gain per time. Individual differences
among conspecifics in their abilities to exploit different
prey have important implications regarding intraspecific
competition. Individuals with similar skills or preferences
would encounter the strongest competition, while competition
would be weakest among those animals that prefer different
foods.

What relevance do results from laboratory experiments
such as Partridge's (1976) and Krebs et al.'s (1977)
have for the field situation? Prey selection is influenced
by many factors which are often not encountered or impossi-
ble to simulate in the lab, such as weather-dependent
foraging, the effect of anti-predator behaviour on the
allocation of time for feeding, etc. However, an ability
to make decisions about optimal prey choice in laboratory
experiments could only have been acquired through the
process of natural selection operating in the real world.

THE STUDY PROBLEM

The present thesis developed from an observational
study, based on previous work by Montevecchi (1979), of
predator-prey interactions between Common Ravens (Corvus
corax) and Blacklegged Kittiwakes (Rissa tridactyla) in a
seabird colony on Baccalieu Island, Newfoundland. An attempt

was made to quantify the predatory activity and success of the ravens, as well as to examine kittiwake nest defense. The hunting behaviour of a pair of territorial ravens was considered in terms of energetic costs and benefits using published data on raven body weight and energy requirements, and biochemical assay of the caloric value of prey.

In an effort to investigate the energetics of corvid foraging and feeding behaviour in finer detail with reference to predictions of O.F.T., the following series of field experiments with Gray Jays (Perisoreus canadensis) and Common Crows (Corvus brachyrhynchos) was undertaken. These experiments simulated a rapidly depleting food patch within which foraging requires prompt decision-making. There was no concern in this study with the survival value of foraging behaviour.

As discussed earlier, O.F.T. consists of related economic models through which an animal's feeding efficiency may be expressed by the relationship between its total energy gain, E, and total foraging time, T. Initially, two different sizes of a single food were offered, which meant that energy per bait, e, was variable, while handling time per bait, t, was about the same.

In later experiments E and T were both varied as bait types of different energy values and handling time requirements were offered.

Several components of foraging time, T, were manipulated in three different experiments: search, handling, and recognition times were increased in an effort to induce switching, as predicted by O.F.T. The final experiment, which involved a predator model, required two levels of decision-making; the jays first had to decide whether or not to feed, and if so which foods to take.

Jays and crows are opportunistic feeders and both, particularly the former, maintain close associations with man. Owing to this circumstance, the choice of human foods for experimentation seemed appropriate. Trials were run in a picnic area or along cabin roads where similar foods were probably encountered regularly.

Because corvids are avid food hoarders (Goodwin 1976) and baits were rarely eaten during trials, satiation was not a factor in the foraging behaviour of either species. The birds made continuous trips to the feeding area until all baits had been taken, and during trials they were not observed to take any food other than what I offered. To

partially compensate for the fact that the relationship between large and small baits, and between different bait types, constantly changed as baits were removed from the population, only the first 50% of the birds' choices in each trial were analyzed. This data analysis technique has been used in other feeding studies (e.g. Manly, Miller and Cook 1972; Bantock and Harvey 1974; Horsley et al. 1979). In addition, the justification of discussing intergroup as well as individual (intragroup) differences among three birds is that Gray Jays tend to remain in small family groups (Lawrence 1973); thus, these experiments actually represented the bait preferences of an entire group of birds.

Throughout this thesis, the terms 'predator' and 'prey' are used in a general sense to denote the jays and crows, and artificial baits, respectively. "To a seed, a finch is as much of a predator as a shark is to us." (Krebs and Davies 1978, p.35).

O.F.T. predicts that animals should be non-selective when high quality prey are scarce but should be discriminating when such prey are abundant (e.g. Ward 1965; Goss-Custard 1977a). The reactions of jays and crows to changes in the density of an artificial prey population

were investigated in Experiment 2.

There is strong evidence to suggest that visually
hunting animals, especially raptorial birds, select odd-
appearing prey from a population (e.g. Mueller 1968, 1971).
The crows' reactions to groups of baits which contained
one odd prey item were tested in Experiment 3. Because
predatory behaviour has been well documented among
corvids (e.g. Aspden 1928; Tinbergen et al. 1962; Mon-
tevecchi 1976a, 1979), and because prey oddity may play
a role in the feeding behaviour of these birds, selection
of odd items may have influenced some of the bait choices
in the previous experiment.

Crypsis is a widespread anti-predator strategy
(e.g. Croze 1970; Montevecchi 1976b), and because later
experiments are predicated on the assumption that cryp-
ticity affects foraging time and thus prey selection, the
presumed survival value of dispersal by cryptic prey
was studied in Experiment 4. Croze (1970) found that
cryptic prey enhance survival by increasing inter-
individual distances, though this benefit does not accrue
to non-cryptic prey. This finding was explained in
terms of the interindividual distances of cryptic prey
exceeding the direct detection distance (D.D.D.) of a

visually hunting predator, while those of non-cryptic
prey did not.

As previously mentioned, food quality may be an im-
portant factor in an animal's foraging strategy; however,
there is a scarcity of information dealing with food
quality as a complicating factor in prey selection (Pulliam
1975). In view of previous studies (Moss 1968; Estabrook
and Dunham 1976), it was anticipated that the jays should
be able to select foods in terms of net energy, E/T.
Norberg (1977) predicted that search effort should be
less costly when an animal forages for low quality or
scattered prey, and conversely, when prey is abundant
or of high quality, the predator should invest more time
in search effort because potential gains are high. Goss-
Custard (1970), and Goss-Custard and Rothery (1976)
found variable search rates to be a feature of the for-
aging strategies of Redshank and Oystercatchers
(Haemotopus ostralegus), and Evans (1976) noted that
Bar-tailed Godwits (Limosa lapponica) use less costly
foraging methods when prey densities are low. Experiment
5 examined the preferences of jays between pairs of food
types which differed in energy value, nutrient content,
handling time requirements, and crypticity.

As increased search time caused by crypticity decreases the profitability of a food, it was anticipated that the jays would switch to a less preferred, though more conspicuous bait type.

Because specific nutrient requirements (e.g. Emlen and Emlen 1975; Goss-Custard 1977b) and individual differences (e.g. Partridge 1976) may affect food choice, the foraging of three known jays among three foods offered simultaneously was considered in terms of energetic costs and benefits in Experiment 6.

Because the energy requirements (Vechte 1964; King 1974) and food preferences (Lawrence 1973) of the jays probably vary throughout the year, separate measures of bait selections taken in autumn, winter and spring were compared.

In general, if a predator's efficiency in dealing with a particular prey changes, an optimal strategy is to switch to another prey (Murdoch 1969; Hughes 1979). Increased handling time may alter the profitability of a preferred prey, causing prey of lesser value to be included in the optimal diet (see Smith and Dawkins 1971).

In Experiment 7, handling time for preferred baits was increased in the presence of easily obtainable al-

ternates, and the selections of three known jays were
studied.

Mimicry, when two species resemble one another in
appearance, odour or behaviour, is a widespread anti-
predator strategy (Alcock 1975). Batesian mimicry
involves deception of the predator by a non-noxious
mimic of a poisonous prey species, whereas Müllerian
mimicry is the resemblance to one another of two noxious
species. Presumably, the predator must learn to avoid
fewer types of inedible prey (Brower 1971). Not all
members of a noxious species are in fact unpalatable,
and those edible individuals that gain an advantage by
resembling inedible conspecifics are called 'automimics'
(Brower 1969). Predators have no way to distinguish
between the two except by taste. Incorrect prey iden-
tification may produce long recognition times, causing
low quality prey to be taken even though more valuable
prey are abundant (Hughes 1979). In Experiment 8, pre-
ferred baits were mixed with inedible mimics in an effort
to increase recognition time and induce switching.

Predator pressure is a different type of constraint
on an animal's foraging behaviour than those examined
in previous experiments. Because anti-predator defense

has been shown to affect other aspects of a prey species'
behaviour (Curio 1976), the effects of a predator model
on the feeding responses of a family of jays was in-
vestigated in Experiment 9. It was anticipated that
feeding behaviour would be severely disrupted in favour
of anti-predator activity, especially because alarm
calling and mobbing may successfully reduce predation to
both adults and their offspring (Hartley 1950).

EXPERIMENT 1

Raven Predation in a Colony of Cliff-Nesting Seabirds
and Anti-Predator Behaviour by Black-legged Kittiwakes.

Nesting on cliffs by seabirds reduces predation
(Cullen 1957; Tuck 1961; Nelson 1978) though some
predators are often successful against cliff nesters
(e.g. Perry 1940; Lockie 1952; Montevecchi 1979;
Maccarone and Montevecchi submitted). Black-legged
Kittiwakes (Rissa tridactyla) are probably derived
from a ground-nesting gull, and their adaptions to
cliff-nesting were presumably anti-predator in origin
(Cullen 1957). Reliance upon the safety of the cliff
has caused kittiwakes to abandon many of the usual
Larid defense mechanisms, such as removal of eggshell

fragments and defaecation away from the nest (Cullen 1957;
see also Tinbergen et al. 1962; Montevecchi 1976c). Kitti-
wakes have also been reported to rarely attack predators,
and evoking any anti-predator behaviour is difficult
(Cullen 1957; but cf. Andersson 1976; Montevecchi 1979).
Kittiwakes' eggs have retained their cryptic colouration,
though in contrast to the young of ground-nesting gulls,
chicks are conspicuous in colour and behaviour (Cullen
1957).

This study presents observational data on the pre-
datory behaviour of a pair of territorial Common Ravens
(Corvus corax) on cliff-nesting seabirds, and the possible
role of active nest defense by kittiwakes in reducing
predation. Hunting behaviour is considered in terms of
energetic costs and benefits, and the ravens' success
is compared to that of other corvids.

METHOD

In June and July 1979, 63 hr of observation were
made in kittiwake colonies in Bull Gulch, where approx-
imately 2000 pairs nest, on the eastern side of Baccalieu
Island (48°07'N, 54°12'W), Newfoundland (Figures 1 and 2).
Most observations were made in the morning or early
afternoon from a distance of approximately 150 m.

A patrol was recorded whenever a raven was judged.

Figure 1. Map of Baccalieu Island and its location off Newfoundland (a, inset). Observations of raven predation were made at cliffs in Bull Gulch (b).

Newfoundland

(a)

Light

Baccalieu Island

Labrador Sea

Puffin Island

Gannet Head

(b)

Lighthouse

N

Scale: 1cm : 200m

0   1000m
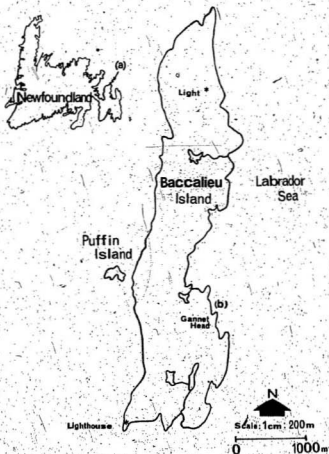
Figure 2. Photograph showing study cliffs above Bull
Gulch on Baccalieu Island.

to fly within 10 m of cliffs where kittiwakes nested.
These data were recorded: a) frequency of patrols, b) num-
ber of ravens per patrol, c) frequency and number of kitti-
wakes displaced from cliffs, d) whether ravens landed in
the nesting area, e) frequency of patrolling ravens chased
by kittiwakes, and f) predation success.

Cost/benefit anaylsis of the ravens' hunting behaviour
is based on these assumptions: a) body weight=1.05 kg, from
published data on *Corvus corax principalis* (Lasiewski and
Dawson 1967; Coombes 1978), b) BMR=4.95 kcal/hr, obtained
from the equation BMR=4.78 $W^{0.726}$, where W is body weight
in kg (King 1974), c) cost of flight=8.0x BMR (Bernstein,
et al. 1973; Berger and Hart 1972), d) average patrol dur-
ation of 30 sec, recorded during observations, e) daily
energy expenditure (D.E.E.) = 328.8 kcal/bird/24 hr, ob-
tained from the equation log DEE=log 317.7 + 0.7025 log W,
where W is body weight in kg (Kendeigh 1970), f) caloric
value of prey, obtained by bomb calorimetry, are: kittiwake
egg, less shell, mass=36.0 g, 69.5 kcal; small chick, less
feathers, mass=47.1g, 45.7 kcal; large chick, less feathers,
mass=155.6 g, 166.5 kcal, g) observation of patrol pattern
and flight path suggested that the ravens which patrolled
in the present study were always the same mated pair that

nested at the base of an adjacent cliff. Furthermore, two
of the three chicks were removed from this nest on 5 June,
and after the remaining chick fledged on 27 June, three
ravens were often seen in trees above the observation cliff.

RESULTS

Sixty-nine percent (117/168) of the patrols involved
a single raven, while two birds patrolled 30% (50) of the
time (χ^2=35.93, df=1, p<0.01). On 5 June, four ravens
approached the observation cliff from the north side of the
island, patrolled once along the cliff and departed. This
was the only observation of a patrol involving more than
two ravens, and was not included in the analysis.

The ravens averaged ($\pm$ S.D.) 2.96$\pm$1.1 patrols/hr, and
there was a slight decrease in patrol frequency throughout
the daily observation period, though this trend was non-
significant (Table 1). Overall, 93% of patrols caused kitti-
wakes to leave the cliffs, 91% of the patrols by single
ravens and 98% of those by pairs. Single ravens caused an
average displacement of 11.9$\pm$ 8.8 kittiwakes, compared to
14.0$\pm$ 5.0 when two birds hunted. Neither the percentage of
patrols that resulted in displacement nor the number of
kittiwakes displaced per patrol is significantly different
between patrols by singles and pairs of ravens.

Table 1. Patrol frequency by two Common Ravens in a seabird colony at different times of the day. Difference (determined by one-way ANOVA) is non-significant.

Time Interval	Hr Observation	N Patrols	$\bar{X}$ Patrols/hr +S.D.
0500-0800	10	34	3.4± 1.0
0801-1100	27	84	3.1± 1.3
1101-1500	20	51	2.6± 1.1
Total	57	169	
Grand $\bar{X}$± S.D.			3.0± 1.1

On 23% (39/168) of the patrols, one or both ravens landed on the cliff, though not always in the vicinity of a kittiwake nest and were successful during 31% (12/39) of the landings. Ravens vocalized loudly on 71% (120/168) of the patrols and 100% (12/12) of successful ones, significantly more than expected (X^2=9.94, df=1, p<0.01).

Ravens patrolled upper portions of the cliff (49%; 83/168) significantly more than middle (33%; 56) and lower (18%; 30) sections (X^2=25.09, df=2, p<0.01). However, predation success was 20% (6/30) during low patrols, compared to 7% (4/56) and 2% (2/83) on medium and high ones, respectively, though this trend is non-significant.

Neither average patrol frequency nor predation success varied significantly over the season (Figure 3).

Kittiwakes chased ravens on 40% of patrols regardless of patrol size; chases usually involved two or three gulls.

The ravens were observed stealing four eggs and eight chicks (six small, two large) for a success rate of 7.1%. Single ravens were more successful, taking prey on 8.5% of patrols, compared to 4.0% for pairs, a significant difference on the basis of equal success expectancy (X^2=5.33, df=1, p<0.05).

Figure 3. Frequency of patrolling by two Common Ravens along a colony of cliff-nesting kittiwakes over a five week period. Fledging date for the raven chick was 27 June. Difference in patrol frequencies is non-significant (determined by x^2 test of expected equal frequency). Percentages above bars refer to predation success during each interval. (Differences are non-significant.)
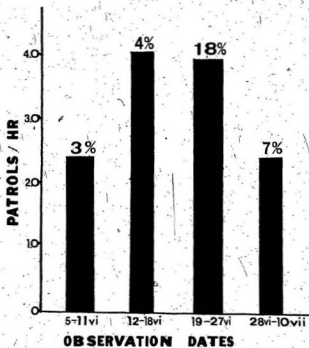
The results of the cost/benefit analysis are shown in Table 2. Net energy gain, E/T, averaged 1.05 kcal/hr above estimated maintenance and foraging costs. It required a single raven an average of 4.69 hr, 14.1 patrols and 66.5 kcal to obtain each prey, which contained an average of 73.8 kcal.

DISCUSSION

Ravens typically patrolled alone, along upper portions of the cliff, though they achieved greater success when they hunted at lower altitudes. Updrafts may have enabled the ravens to expend less energy searching for prey higher on the cliff and to observe more nesting birds. Turbulent eddies, caused by swirling winds, and the danger of being blown or chased into the sea or the cliffs, may have prevented the ravens from exploiting nests at the base of the cliff,more often. Moreover, ravens may have only flown lower after potential prey were sighted from above (see also Montevecchi 1979).

The mean of 2.96 patrols/hr was relatively constant throughout the day and similar to the hunting frequency of 3.3 patrols/hr observed along the same cliff in 1976, but considerably lower than in 1977, when ravens average 14.3 patrols/hr (Montevecchi 1979). As many as six ravens in a

Table 2. Results of cost/benefit analysis of Common Raven predation on kittiwakes.

Energy Gains:

Source	Number	Energy/Prey(kcal)	Total Energy(kcal)
Egg	4	69.5	278.0
Small Chick	6	45.7	274.2
Large Chick	2	166.5	333.0
Total	12	$\bar{X}=73.8$	885.2

Energy Costs: Time-Budgeting Method considers costs of patrolling and non-flight activities.

Total Bird-Patrols-

Single	Paired	x $\bar{X}$ Patrol Time	x BMR(kcal/hr)	x Coef. of Flight (Berger and Hart 1972)	Subtot. =(kcal)
117	+ (2)50	0.5 min	4.95	8.0	4.6

Non-flight Activities-

Time(hr)	x N Birds	x BMR(kcal/hr)	x Coef. of Existence(King 1974)
61.2	2	4.95	1.24

Total Costs= 6

Balance= 65.6

patrol and up to 20 on the cliffs were observed in 1977, whereas in the present study mean patrol size was 1.3, and on only one occasion did more than two ravens hunt.

With the assumption of a territorial mated pair in the present study, it is feasible that food sharing between adults (Goodwin 1976) and feeding of offspring, may have influenced the ravens' hunting intensity, and that territorial defense may have determined patrol size. Raven flocks tend to be composed of non-breeding and non-territorial birds (Goodwin 1976), and it is possible that the more intensive hunting by larger flocks observed in 1977 (Montevecchi 1979) may have reflected individuals of this status. This of course does not explain the low patrol frequency observed in 1976 (Montevecchi 1979).

Montevecchi (1979) also found a direct relationship between hunting success and group size, and speculated that a switch to group hunting could increase the ravens' efficiency. Yet, in the present study, predation success by single ravens was more than twice as great as when two birds hunted.

Kittiwakes were not observed to be the submissive victims described by Cullen (1957) and instead vigorously defended their nests, often chasing and diving at the ravens,

which apparently lowered predation success. Montevecchi
(1979) noted an increase in kittiwake nest defense from
1976 to 1977, which correlated with increased hunting in-
tensity and predation success by ravens. In the present
study, lower levels of patrolling and kittiwake anti-
predator behaviour were found. It seems that hunting in-
tensity and predator defense are directly related.

The ravens' predation success of 7.1% is similar to
that observed by Montevecchi (1979) in the same colony.
Jackdaws (Corvus monedula) showed a 3.5% success rate in
Common Murre (Uria aalge) colonies (Birkhead 1974) and
from the number of preyed upon eggshells of this species
found on Baccalieu Island (Montevecchi, unpub.data; Mac-
carone, unpub.data), ravens apparently have a low success
against this species as well. Carrion Crows (Corvus corone)
have a low success rate in Black-headed Gull (Larus ridibun-
dus) colonies, probably because their attacks directed at
eggs and broods are effectively repelled by adults (Kruuk
1964).

The ravens probably obtained sufficient energy to meet
their own requirements and to feed the remaining chick.
Had the full brood of ravens been left intact, it is feasi-
ble the frequency of patrolling would have been greater to

meet this additional cost. In terms of economic costs and benefits, raven predation on kittiwakes appears efficient, although the limited number of prey taken during brief observation times allowed only crude analysis. The following series of experiments with Gray Jays and Common Crows attempts to analyze corvid foraging and feeding behaviour more closely.

EXPERIMENT 2

Bait Selection as a Function of Relative and Absolute
Density.

As indicated previously, prey density has been shown
to greatly affect a predator's diet. Change in absolute
density refers to an increase or decrease in the total prey
population, where the proportion of profitable prey remains
the same, whereas relative density describes fluctuations
in the percentage of profitable prey in a population of con-
stant size. At high absolute prey densities, animals gene-
rally become more selective. The importance of the relative
abundance of profitable prey, that is, their proportion of
a total population, is unclear. Theoretical models suggest
that frequency dependent predation should depend on absolute
prey density (Clarke 1962; Horsley et al. 1979), though pas-
serines have been shown to prey more heavily on common prey
types, independent of density (Allen and Clarke 1968).

Feeding experiments that manipulate prey abundance
usually produce a characteristic S-shaped curve (Curio 1976),
described by Holling (1965) as a Type 3 functional response.
Such a function indicates that as the absolute density of a
preferred prey increases, the number of less favoured foods
eaten will decrease, while the total amount of food eaten

remains relatively constant.

The present experiment investigated bait selectivity of corvids as functions of absolute and relative densities of profitable bait types, and it was predicted that the birds would become increasingly more selective as functions of both types of density increase.

METHOD

Free-living Common Crows and Gray Jays were tested in Father Duffy's Well (47°15'N, 53°18'W), a small provincial park located 62 km SW of St. John's. Trials with jays involved three birds and were run on a picnic table with an approximate 2 m^2 surface (Figure 4). Observations were made from 5 m. Occasionally, jays were attracted to the feeding area by a recording of a Gray Jay alarm call. In trials with crows, baits were spread randomly over a 2 m^2 area on the ground; usually five, and as many as seven birds fed during these trials. Owing to their wariness, crows were observed from 50 m with 7x35 mm binoculars. Jays and crows were tested on different days to avoid interspecific competition. Birds were not individually marked so it was impossible to determine individual differences in bait selection.

Two designs were used to test the birds' responses to

Figure 4. Gray Jay taking a bait from the picnic table during feeding trial.

changes in prey abundance: 1) density trials offered bait populations which contained equal numbers of both large and small baits in abundances of 4, 8, 12, 16, and 24 items, 2) frequency trials offered populations which were comprised of 14, 25, 33, 50, and 75% large baits and always contained 12 items, except 14 on 14% trials. Each species was tested for eight trials at each level of density and of frequency. Large baits were whole Saltine crackers. The caloric value of Saltines is 4.1 kcal/g (Albritton 1954); large baits being 12 kcal, small ones 6 kcal.

RESULTS

Both species were increasingly selective as absolute density increased, though significant selectivity occurred at a lower density for crows than for jays. At a density of $6/m^2$, the crows took significantly more large baits than was expected by chance ($\underline{x}^2 = 4.08$, df=1, p<0.05), while significant discrimination was first shown by jays at $8/m^2$ bait density ($\underline{x}^2 = 4.00$, df=1, p<0.05). The difference between the two species is significant (one-tailed, $\underline{t} = 3.13$, df=14, p<0.01). At lower densities, both species were non-selective (Figure 5).

In relative density trials, an increase in the percentage of large baits was followed by increased selectivity by both species (Figure 6). Crows had an earlier threshold

Figure 5. Percentage of large baits taken as a function of bait density by Gray Jays and Common Crows. Selections that differed significantly from chance (determined by x^2 tests of 50:50 expectancy) are indicated.

Axis labels: % LARGE - BAITS TAKEN (vertical), DENSITY (BAITS/M²) (horizontal)

Curve labels: jays, crows

Legend: ** $p < 0.01$, * $p < 0.05$

chance line at 50
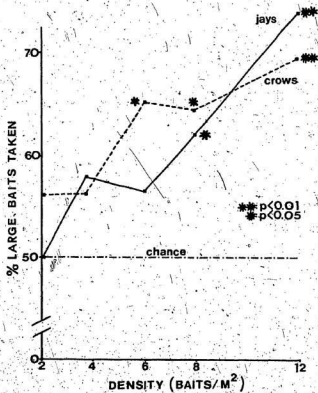
Figure 6. Percentage of large baits taken as a function of their proportion of the total population by Gray Jays and Common Crows. Selections that differed significantly from chance (determined by x^2 tests on the proportions of large baits offered and taken) are indicated.
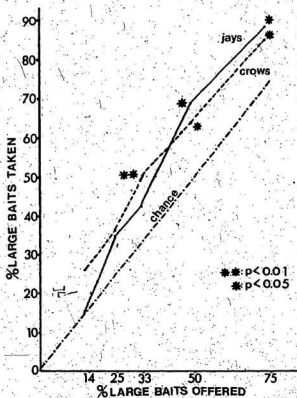
in this condition also. When the ratio of large to small baits was 1:2, crows took significantly more large ones than expected (x^2=12.00, df=1, p<0.01), whereas the jays did not do so until this ratio was 1:1 (x^2=6.75, df=1, p<0.05). The difference between the two species is significant (one-tailed, t=4.31, df=14, p<0.01).

DISCUSSION

Jays and crows responded to changes in an artificial prey population by increasing selectivity as the absolute and relative densities of profitable baits increased. The crows appeared more sensitive to density and frequency changes than the jays, as suggested by their earlier tendency to select large baits in both conditions. In the present experiment, approximations of the Type-3 response were apparent in the bait selections of both species in the density condition (Figure 5), and by the jays in the frequency condition. Crows consistently took a higher percentage of large baits than were offered (Figure 6).

The interspecific differences may be due to the number of individuals and feeding behaviour of crows and jays. Typically, three jays fed simultaneously, and their small bills (30 mm, Gwinner 1951) enabled them to take only one bait/trip. Crows tended to feed in larger flocks in which

overt aggression and food stealing resulted in a higher
level of competition than occurred among jays. The crows'
larger bills (62 mm, Gwinner 1951) and wider gape enabled
them to take up to four baits/trip. As a consequence,
crows may have been subjected to greater pressure to select
baits more efficiently and quickly.

Even at the highest absolute and relative densities
of large baits, some small crackers were always selected dur-
ing the early stages of each trial. This response contra-
dicts a basic prediction of O.F.T., namely that a particular
food, or size class of a single species, is taken whenever
it is encountered or else not at all (Emlen 1966; Pearson
1974; Charnov 1976). In fact, this all-or-none selectivity
has never been shown to occur; rather, a smooth curve, which
reflects a gradual increase in selectivity, invariably re-
sults. This functional response has been explained in terms
of sampling (Krebs et al. 1977): an animal monitors its food
environment to assess the availability and profitability of
different prey. In doing this, a certain amount of effici-
ency is sacrificed. The importance of relative prey density
to food selection and optimal diet is not clear. Rapport
(1971) argues that this is an important characteristic of
a prey population, while Pulliam (1974) feels that only the

absolute density of the preferred prey can shape the optimal diet. More extensive, long term studies are needed to help clarify this matter.

EXPERIMENT 3

The Effect of Oddity on Prey Selection.

Prey oddity takes at least three forms (Curio 1976):
1) spatial oddity, as when individuals stray from a group,
2) movement, varying from slight abnormalities in locomo-
tion to panic flights, and 3) deviant morphological appea-
rance, i.e. colour, size, orientation, etc. Selection
against odd or conspicuous prey has been observed in the
field. Peregrine Falcons (Falco perigrinus) selectively
attack birds which have become separated from the flock,
and Goshawks (Accipiter gentilis) select feral pigeons which
differ in colour from other flock members (Pielowski 1959).
It is apparently easier for a predator to fix its attention
on an odd-appearing prey (Curio 1976). Experimental evi-
dence also supports selection against odd prey: captive
American Kestrels (Falco sparverius) disproportionately
selected odd prey that differed from the rest of the popula-
tion, but not against conspicuous prey that differed from
the background (Mueller 1968, 1971).

A question that remained after Experiment 2 was whether,
in the frequency condition, the birds were selecting the
most common bait size rather than increasing discrimination
as large baits became more abundant. It is possible that

oddity is an important criterion of food selection by corvids, and in the present experiment, populations of artificial baits containing an odd member were presented to crows.

METHOD

Unmarked, free-living Common Crows were tested in the provincial park study area. Artificial prey were whole Saltine crackers and hand-moulded Ken-L-Ration dog food, both 2.8 g. On 20 trials, nine crackers and one meat bait were spread randomly over a 2 m^2 snow-covered area, and on 20 trials nine meat baits and one cracker were simultaneously offered. Trials were randomized with respect to presentation of odd items. While not as conspicuous as meat baits, pilot trials indicated that cracker baits were visible on the snow to the crows. Birds were allowed to feed until depletion of all baits, though only the first bait taken in each trial was considered in the analysis (Mueller 1968). Observations were made from 50 m with 7x35 mm binoculars (Figure 7).

RESULTS

Crows first selected odd baits in both conditions (Table 3). Baits that differed from the rest of the population suffered significantly higher predation than was expected by their proportion to the total sample (X^2 =67.20, df=1, p<0.01). In both conditions, odd baits were taken first on 13 trials.

Figure 7. Common Crows selecting baits during feeding trials that offered artificial bait populations which contained one odd member.

Table 3. Design and results of an oddity experiment in which Common Crows were offered artificial bait populations that contained one odd member. M= meat baits; C= crackers.

Condition	No. Trials	Offered Each Trial M	C	First Choices(tot) Expected M	C	Observed M	C	X^2	P
Meat Odd	20	1	9	2	18	13	7	67.2	0.01
Crackers Odd	20	9	1	18	2	7	13	67.2	0.01

Of the 10 baits per trial, odd meats were chosen with a rank ($\pm$ S.D.) of 2.2$\pm$2.1 and odd crackers 3.1$\pm$3.0.

DISCUSSION

Oddity, in terms of deviant morphological appearance, may be one criterion of food selection in crows. This appeared to be so when baits were odd in colour and/or shape. It now seems more plausible that, on reaching a certain threshold, bait selection in Experiment 2 was in fact dependent on the proportion of large baits in the population, as the crows differentially selected odd, not common baits in the present experiment.

These results support Mueller's (1968, 1971) findings for raptorial birds, but conflict with data from Allen (1972) for passerines, which indicate strong selection against common prey. Crows are passerines, though they are classic omnivores and true predators (e.g. Butler 1974; Burger and Hahn 1977; George and Kimmel 1977; Coombes 1978). In this respect, selection against oddity, like that of true raptors, makes good biological sense in corvids.

EXPERIMENT 4

The Effect of Dispersal in Reducing Predation in Cryptic and Non-Cryptic Prey.

Prey crypticity acts to increase a predator's search time and thus influence prey selection. Predator pressure, in turn, causes some prey species to space themselves in such a way that interindividual distances exceed the direct detection distance (D.D.D.) of their most common predator (Tinbergen, Impekoven and Franck 1967). Taylor (1976, p. 489) observed: "Animals which space themselves out from their neighbours will be found by searching predators less often than individuals that fail to do so." Camouflage functions to provide as small a D.D.D. as possible. Crypsis, or resemblance to background, and dispersal are related phenomena, and many authors (e.g. Tinbergen et al. 1967; Taylor 1976) have noted that cryptic prey may reduce their predation by lowering their density. In the present experiment, populations of cryptic and non-cryptic artificial baits were presented at low and high density to visually hunting predators to test the presumed survival value of dispersal.

METHOD

Three known Gray Jays, a juvenile (Bird U) and two adults (Birds B and R), were tested in the provincial park

study area. Artificial prey were rectangular pieces of white salt pork and cylindrically shaped, red Ken-L-Ration dog food (Figure 8). Average($\pm$ S.D.) dimensions, weights and energy value of fat baits were: 19.9$\pm$ 0.4x8.5$\pm$ 0.4x 8.5$\pm$ 0.4 mm, 1.5$\pm$ 0.4 g, and 9.3 kcal, and for dog food baits 28.8$\pm$ 0.5x 8.5$\pm$ 0.3 mm, 1.6$\pm$ 0.1 g, and 6.15 kcal.

Trials were run on a picnic table, on which the jays had been trained to find food. A 10 cm layer of snow covered the table, presumably rendering the fat baits cryptic. Eight trials were run in each of four conditions: Ten of each bait type were offered separately at high and low density. In the 'clumped' condition, baits were spread over half the table, sides being randomly alternated; in the 'dispersed' condition, baits were scattered over the entire table. Trials ended when all baits had been removed. Search and handling time, defined as the interval between landing on the table and flying off with a bait, were recorded.

RESULTS

There were significant increases in mean search and handling time and in total bait depletion time when the jays searched for cryptic baits that were dispersed as compared to clumped. Total depletion time for dispersed fat baits was 87.5$\pm$ 5.6 sec, and for clumped fat baits 47.9$\pm$ 2.0 sec

Figure 8. Fat (on right) and meat baits on snow dur-
ing crypsis trials.

(F 1,14=42.79, p<0.001). No increase in depletion time occurred when the non-cryptic dog food baits were dispersed (39.0± 3.9 sec) compared to when they were clumped (38.8± 3.1 sec; see Figure 9).

Depletion times for meat baits were significantly shorter than for fat baits when each occurred at low density (F 1,14=55.71, p<0.001), though not when they were clumped (F 1,14=4.09, p>0.05). Search times for individual birds were similar within a condition and so were combined. Table 4 shows mean (± S.D.) search time and total numbers of baits taken in each condition by the three jays. The total baits taken differed significantly among birds from the expected equal selection in both dispersed (x^2=23.10, df=2, p<0.01) and clumped trials (x^2=10.60, df=2, p<0.01). Bird U took significantly fewer baits than the other jays (F 2,9=57.10, p<0.01). Mean search times for dispersed fat baits were longer than for clumped fat baits (F 1,4=19.10, p<0.025) and for clumped (F 1,4=14.51, p<0.025) and dispersed meat baits (F 1,4=13.20, p<0.025). Mean search times for dog food baits did not differ between density conditions.

DISCUSSION

Crypsis alone was not sufficient to reduce predation by the jays; spacing of prey was also important. Within the limitations of the present experiment, decreased predation

Figure 9. Mean depletion time (sec) for cryptic (fat) and non-cryptic (meat) baits by Gray Jays in two density conditions. Significant differences (determined by subject-by-trials ANOVA) are indicated.

** : p<0.01

DEPLETION TIME (SEC)

FAT   MEAT   FAT   MEAT
  'CLUMPED'   'DISPERSED'
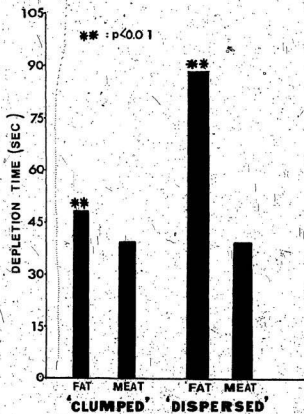
Table 4. Mean (± S.D.) search times (sec.) and total number of baits taken by three Gray Jays in two density conditions.

Bird	Fat Baits				Meat Baits			
	Dispersed		Clumped		Dispersed		Clumped	
	Search	N Baits	Search	N Baits	Search	N Baits	Search	N Baits
U	11.0±5.8	15	4.7±2.1	19	6.3±0.9	10	4.0±1.0	15
B	7.8±4.6	37	5.4±2.5	33	4.2±2.2	34	5.3±2.1	29
R	8.9±1.3	28	5.0±1.9	28	3.6±0.9	36	3.3±0.8	36
Total		80		80		80		80
Grand X̄	9.2±0.3		5.0±0.1		4.7±0.3		4.2±0.3	

is not gained by conspicuous baits when their density is reduced. These results concur with previous studies by Croze (1970), Andersson and Wiklund (1978) and others. Although depletion times were measured in the present experiment, the implications would be similar had trials been terminated after a fixed interval. When prey become more difficult to find, a predator must allocate more time to foraging and less to other behaviour. Goldcrests (_Regulus regulus_), for example, have been estimated to devote 100% of their time to food gathering in winter (Gibb 1960).

EXPERIMENT 5

The Role of Food Quality in Selection When Two Foods Are Offered Simultaneously.

As mentioned in the General Introduction, O.F.T. predicts that animals have the ability to differentially select prey in terms of net energy value, E/T (Schoener 1971). If the relationship between energy, E, and time, T, changes for a particular prey type, an animal may switch to alternate foods. One cause of switching is an increase in search time for preferred prey. In the present experiment, the ability of wild birds to differentially select foods on the basis of caloric value and their willingness to switch from a preferred bait type when it became difficult to find were investigated. In addition, foraging effort in relation to potential energy gains was examined.

METHOD

Three known Gray Jays were tested in the provincial park study area. Three baits were used: rectangularly cut salt pork, hand-moulded Ken-L-Ration dog food and halved Saltine crackers (see Figure 10).

The organic composition of foods can be expressed as the percentages of fat, protein, carbohydrate, water and ash, totaling 100%, though energy available to the consumer

Figure 10. Baits used in feeding experiments: (a) fat
(b) meat (c) cracker.
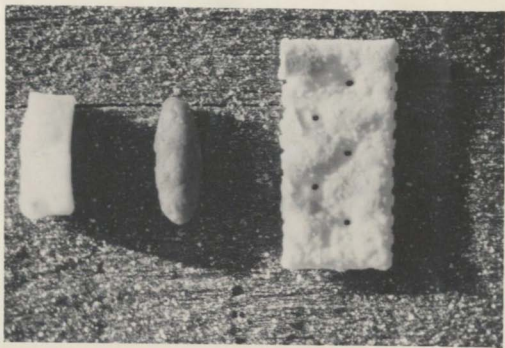
(a)   (b)   (c)

is stored only in fat, protein and carbohydrate. Food
types were chosen on the basis of differences in organic
composition (Table 5). Organic analysis was used to
determine the assimilable energy of each bait type: salt
pork - 9.3 kcal, dog food - 4.05 kcal, and Saltines -
6.15 kcal. For convenience, these foods are referred to
as fat, meat and crackers, respectively.

PROCEDURE

Jays were offered the three possible paired combin-
ations of baits. To investigate the effect of crypsis on
bait choice and search time, 16 trials were run for each
paired combination, half on the bare picnic table, half
when snow, usually 5-10 cm, covered the table. In the lat-
ter condition, baits were set on the snow, not pressed into
it. Each trial began with 20 baits, 10 of each type, spread
randomly over the 2 m^2 surface. Bait pairing was randomized
across trials, which were terminated after all baits had
been removed, or 10 min after the first jay landed on the
table. A trial was considered to be half completed when 50%
of the total energy (kcal) had been removed from the table.
Because of the differences in energy value between bait
types, efficient bait selection would produce depletion
times for 50% of the total energy that were shorter than

Table 5. Organic composition of foods used in feeding experiments. Maximum component values are underlined.

| Food | % Composition | | | | |
	Protein	Fat	Carbohydrate	H$_2$O	Ash
Salt Pork	9.5	65.2	0.5	20.1	4.7
Ken-L-Ration	20.8	8.6	27.5	36.5	6.6
Saltines	9.0	9.0	73.0	9.0	0.0

would be expected with random selection. In the analysis
of bait preference, only the initial 50% of the birds'
choices were considered.

RESULTS

Though there was great individual variation among
jays, fat was preferred overall in the 'no snow' condition
to both meat and crackers (x^2s=8.84 and 61.95, respectively,
dfs=1, ps<0.01); there was slight, but non-significant
selection for meat over crackers. During trials on snow,
the increase in meat preference was significant (one-tailed,
t =4.37, df=7, p<0.01), though meat was not taken more often
than fat in this condition. Similarly, crackers were not
chosen over fat baits in the crypsis condition, but increased
from 6 to 40% of initial choices (one-tailed, t=11.07, df=
7, p<0.01). When meat and crackers were offered together,
there was no differential selection between substrate condi-
tions (Table 6).

Foraging effort was greater during initial portions of
trials and gradually waned as more baits were removed. It
required a mean (± S.D.) of 44.0± 10.2 sec to remove half
the food energy contained in fat/cracker populations, signi-
ficantly shorter than would be expected had selection been
random or had proceeded at a constant rate (x^2=238.60, df=1,

Table 6. First 50% bait choices of Gray Jays in two sub-
strate conditions. Significant differences (determined by
one-way t-tests) are indicated. F=fat; M=meat; C=crackers.

	Substrate Condition			
Baits Offered	No Snow	Snow	% Change	t
Fat and Meat	53F:27M	38F:42M	-20	4.37**
Fat and Crackers	75F: 5C	48F:32C	-34	11.07**
Meat and Crackers	53M:47C	55M:45C	+ 3	1.00

**: $p < 0.01$

$p < 0.01$). Mean (±S.D.) times required to gather half the energy contained in fat/meat (85.8± 89.7 sec) and meat/cracker populations (191.3± 73.5 sec) were also significantly shorter than expected ($\overline{X}$ s=126.30 and 19.40, respectively, dfs=1, ps< 0.01; Figure 11).

DISCUSSION

The jays tended to differentially select ranked foods according to energy content, preferring fat to alternates. Meat baits were, however, selected slightly more often than calorically more valuable crackers, and this trend warrants closer examination. It may well have been that differences in handling capabilities caused fat and meat baits to be more profitable than crackers: an average of two fats or meats were taken per trip, compared to only one cracker. It is possible that the jays selected foods in terms of their net energy, E/T, rather than in descending order of gross energy (Rapport 1971; Pyke et al. 1977). Excluding the strong fat preference the results are not compelling: the slight preference for meat accounted for only eight more of this food being taken than crackers.

When potential energy gain was great, feeding behaviour was vigourous and return times short. Foraging became less intense as more profitable baits were removed from the table.

Figure 11. Percentage of total depletion time required
to obtain half the energy (kcal) contained in three
mixed populations of baits. All times are significantly
shorter than expected on the basis of a constant foraging
rate with random selection.

BAITS OFFERED
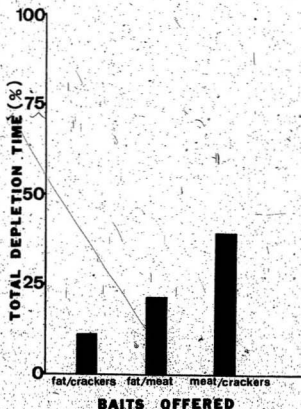
Rapid depletion of 50% of the energy in bait populations is also indicative of efficient food selection as high calorie baits were selected first. Bird R's choices may have been shaped by competition from the other jays. In the 'no snow' condition this bird took mostly meats, while the other jays preferred fat. It seems reasonable that Bird R would continue to take meat baits when fats became cryptic. In the 'snow' condition, however, Birds U and B switched to meat, and R to camouflaged fat. Interestingly, the switch to fat resulted in increased foraging efficiency. Competition from the other jays may have prevented Bird R from exploiting fats in the 'no snow' condition, though it is unlikely Bird R would be subordinate to Bird U, a juvenile. The social dynamics of Gray Jay families requires further study.

EXPERIMENT 6

The Role of Food Quality in Selection When Three Foods Are Offered Simultaneously.

Domestic chicks and pigeons are able to choose from a variety of foods to yield a balanced diet (Dove 1935; Brown 1969), though exceptions have been noted (e.g. Emlen and Emlen 1975; Goss-Custard 1976). Apparently, not all animals select foods in an efficient manner or have need to (e.g. Marten 1973).

In the previous experiment, the jays selected paired combinations of foods in relation to net energy value. The present experiment offers three different foods simultaneously, imposing a more difficult test of decision-making. The jays are expected to take baits in proportion to their net energy values. Some trials were run on a snow background, rendering the highly preferred fat baits cryptic, which was expected to cause switching to alternate foods. A cost/benefit analysis was applied to the foraging behaviour of three known jays in two substrate conditions.

Lawrence (1973, p.2) mentions the Gray Jays' "special fondness for meat and fat in the cold season", and in the present study a comparison of trials run in autumn, winter and spring was made to assess seasonal differences in the

jays' food preferences.

METHOD

Autumn trials and winter crypsis trials were run in the provincial park study area with the three known jays; spring trials tested two different pairs of unmarked, adult jays 1 km SW and 5 km NW of the park. Trials in the park were run as previously and with the same three foods. Spring trials were run outside the park and baits were spread randomly over a 2 m² area of level, unpaved road.

Thirty baits, 10 of each type, were offered on each trial, eight of which were run in each substrate condition. Trials ended when all baits had been taken, or 15 min after the first jay landed by the food. The first 50% of the birds' choices were considered in the analysis of food preferences, while entire trial times and choices comprised the cost/benefit analysis. Choices of individuals were noted where possible.

RESULTS

Seasonal differences in fat preference were not found. In four series of trials, fat baits were consistently selected over alternates. Only in the snow trials were meat baits significantly selected over crackers ($X^2 = 6.25$, df=1, $p < 0.02$), though a similar, non-significant trend was evident in non-

snow trials, where 108 meat baits were taken compared to 84 crackers (Table 7).

In autumn trials, two thirds of all fat baits were taken during the first 50% of the jays' selections, compared to half the crackers and a third of the meat baits ($x^2 = 9.80$, df=2, p<0.025). Of their first 50% bait choices, Birds U and B took 50% and 81% fat baits, respectively. Bird R selected meat baits, taking this food 50% of the time. These individual differences in food selection are significantly different from expected ($x^2 = 55.60$, df=4, p<0.01). While individuals differed in choice of foods, the total number of baits taken in the early portions of trials did not differ from the expected one third proportion/bird ($x^2 = 3.20$, df=2, p>0.05; Table 8A).

In trials run on snow, fat baits were again chosen significantly more than alternates ($x^2 = 14.60$, df=2, p<0.01), and meat baits were taken significantly more than crackers ($x^2 = 8.20$, df=1, p<0.01). There were significant differences both in bait preference ($x^2 = 24.19$, df=4, p<0.01) and in the number of baits taken by each bird during initial portions of trials ($x^2 = 6.45$, df=2, p<0.05). Bird B took the fewest baits in the 'non-crypsis' condition, but the most in the snow trials, and Bird R took the fewest baits in the 'crypsis'

Table 7. Seasonal bait preferences of three groups of Gray Jays. Replicate of eight trials for each group. Significant differences (determined by x^2 test of expected equal preference) are indicated.

Group	Season	Substrate	First 50% Choices			x^2	p<
			Fat	Meat	Crackers		
1	Autumn	Picnic Table	54	26	40	9.80	0.01
1	Winter	Snow	56	42	22	14.8	0.01
2	Spring	Gravel Road	61	40	19	22.05	0.01
3	Spring	Gravel Road	53	42	25	9.95	0.01

Table 8. First 50% bait choices of three known Gray Jays in feeding trials in which three foods were offered in two substrate conditions. Figures are totals for eight trials in each condition.

A. Non-crypsis Condition

Bird	Bait Type			Totals	
	Fat	Meat	Crackers	Observed	Expected
U	20	0	20	40	40
B	26	2	4	32	40
R	8	24	16	48	40
Totals	54	26	40	120	120

B. Crypsis Condition

Bird	Bait Type			Totals	
	Fat	Meat	Crackers	Observed	Expected
U	19	3	13	35	40
B	26	26	1	53	40
R	11	13	8	32	40
Totals	56	42	22	120	120

-65-

condition, where before it had taken the most. The forag-
ing effort of Bird B was similar in each condition (Table
8B).

The initial similarity among birds in the number of
baits taken changed as trials progressed. The total num-
ber of baits taken by each jay differed significantly from
the expected one third per capita (χ^2=12.03, df=2, p<0.01).
Foraging effort waned over time for Bird U, as it obtained
68% of its total number of baits in the first halves of
trials, significantly more than would be expected had fora-
ging rate been constant (χ^2=11.36, df=1, p<0.01). In com-
parison, Bird B took only 32% of its total during this per-
iod, significantly less than expected (χ^2=10.87, df=1,
p<0.91).

Bird R's foraging rate was constant over the course of
a trial (χ^2=0.55, df=1, p>0.05; Table 9A). In the crypsis
condition, there was a significant difference in the total
numbers of baits taken by the three birds (χ^2=9.60, df=2,
p<0.01). For two jays, B and R, there were changes in bait
preference. Compared to non-crypsis trials, Bird B took
twice as many meat baits and 85% fewer crackers. At the same
time, Bird R took half as many meat baits and 44% more crac-
kers. The number of fats taken by these birds remained about
the same in both conditions (Table 9B).

Table 9. Total bait choices of three known Gray Jays
in feeding trials in which three foods were offered in
two substrate conditions. Figures are totals for eight
trials in each condition.

A. Non-crypsis Condition

Bird	Bait Type			Totals	
	Fat	Meat	Crackers	Observed	Expected
U	26	6	23	55	80
B	36	27	33	96	80
R	18	47	24	89	80
Totals	80	80	80	240	240

B. Crypsis Condition

Bird	Bait Type			Totals	
	Fat	Meat	Crackers	Observed	Expected
U	24	3	32	59	80
B	40	54	5	99	80
R	16	23	43	82	80
Totals	80	80	80	240	240

A range of foraging efficiencies was found (Table 10). Total energy gain, E, by each bird differed from the expected one third proportion (520 kcal), both in the non-cryptic (x^2=55.80, df=2, p<0.01) and cryptic conditions (x^2=35.10, df=2, p<0.01), and there was no significant change in energy gain by each bird between conditions.

DISCUSSION

No significant seasonal differences were found as fat was consistently preferred to alternates. There was no consistent trend in selection for meat and crackers, but this may be confounded by the effect of crypsis or individual differences. These results contrast with Lawrence's (1973) anecdotal evidence.

In the autumn, the jays selected foods according to gross energy value. Because only one cracker, but several meat baits could be carried per trip, differences in handling capabilities were apparently ignored. In the crypsis condition, possibly due to its high visibility in the snow and more efficient handling, meat baits were taken twice as often as crackers, although fat was again taken most often.

The effect of competition may have been involved in the changes in bait selection by Birds B and R between substrate conditions. When fat became cryptic, Bird B doubled its

Table 10. Results of cost/benefit analysis of feeding trials in which three known Gray Jays were offered three foods in two substrate conditions. Replicate of eight trials.

A. Non-crypsis Condition

Bird	Energy (E) (Kcal)	No. Baits	No. Trips	$\bar{X}$ Return time (sec)	$\bar{X}$ Baits/Trip± S.D.	Foraging Efficiencies	
						E/T (kcal/min)	E/Trip
U	407.6	55	36	65.8	1.5± 0.3	10.1	11.3
B	647.1	96	56	44.8	1.7± 0.4	15.3	11.5
R	505.3	89	52	48.7	1.6± 0.4	11.9	9.7
Totals	1560.0	240	144				
$\bar{X}$				53.1	1.6± 0.4	12.4	10.4

B. Crypsis Condition

Bird	Energy (E) (Kcal)	No. Baits	No. Trips	$\bar{X}$ Return time (sec)	$\bar{X}$ Baits/Trip± S.D.	Foraging Efficiencies	
						E/T (kcal/min)	E/Trip
U	430.8	59	40	96.0	1.5± 0.5	4.6	10.8
B	620.8	99	45	42.0	2.2± 0.5	19.0	13.7
R	508.4	82	69	72.0	1.2± 0.4	5.1	7.3
Totals	1560.0	240	154				
$\bar{X}$				70.0	1.6± 0.5	9.6	10.6

level of selection of meat baits and Bird R switched to
crackers. Direct competition, although likely to be
slight among these birds, depends in part on the distri-
bution of the food supply (Bertram 1978). The high density
at which these baits occurred may have allowed the dominant
bird to choose the best food items. The average return
time of 65.8 sec for Bird U, a juvenile, may be indicative
of its low status. Gray Jays try to hide food out of sight
of other jays that are socially dominant, and may loiter
in the vicinity of caches (Goodwin 1976). Little prior
experience in caching food may have also influenced its re-
turn intervals.

In the non-crypsis condition, individual differences
in bait selection and handling times accounted in large part
for the range of foraging efficiencies. On the snow back-
ground, decreased efficiency was observed for Birds U and
R, but for different reasons. Bird U did not switch to
alternates when fat became cryptic; as a result of increased
search time, its mean return interval increased from 65.8
to 96.0 sec. Efficiency, in terms of energy/time was sharply
reduced. In addition to switching to less profitable crac-
kers, Bird R increased its mean return time from 48.7 to
72.0 sec.

By taking more high quality baits, Bird R's yield of energy/prey increased slightly in the crypsis trials. Bird B increased its efficiency in snow trials by switching to meat and not selecting crackers, as well as being proficient at locating hidden fat baits. By increasing its mean number of baits/trip and maintaining short return intervals, energy/time and per trip were increased.

EXPERIMENT 7

The Effect of Handling Time on Food Choice.

As shown in Experiment 4, an increase in search time could cause a shift in bait choice. Switching may also occur as a result of increased handling time for preferred prey. This experiment examined the role of handling time in the food selection of Gray Jays.

METHOD

Study area, subjects and materials are the same as in Experiment 4. To increase handling time, fat baits were wedged into grooves between slats in the picnic table (Figure 12). Pilot trials showed that the jays were able to extract these baits, though considerable effort was often required. Ten wedged fat baits were offered in each of 16 trials; ten meat baits were also available on eight trials, 10 crackers on the others. Presentation of alternate baits was randomized across trials, which ended after all baits had been taken, or 10 min after the first jay landed on the table. The number of attempts and the time required to extract fat baits were recorded; the first 50% of the jay's choices were used in the analysis.

RESULTS

When fats were wedged in the table, the jays took 64

Figure 12. A fat bait wedged into a groove in the picnic table to increase handling time.
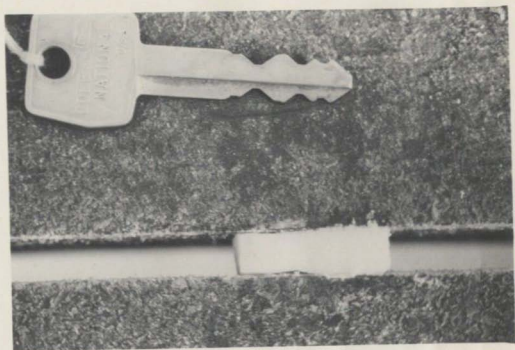
meat baits compared to 16 fats (x^2=28.80, df=1, p<0.01),
though this difference was non-significant when fats were
not wedged, with 42 crackers and 38 fats being taken.
Compared to baseline trials in which handling time had not
been increased, jays took significantly more meat and crac-
ker baits in the present experiment (one-tailed, t_s=-4.38
and -4.15, respectively, dfs=14, ps<0.01).

The jays switched more readily to meat baits than to
crackers, attempting to extract a mean of 1.46 fats for
each meat taken, compared to 3.22 for crackers (one-tailed,
t=-3.20, df=7, p<0.01). This trend, though not statisti-
cally significant, is also seen in the total number of at-
tempts to extract fat baits each trial: a mean (±S.D.) of
15.1 (±4.6) attempts was made to obtain wedged fats when
meat baits were available, compared to 25.2 ±6.6 when crac-
kers were the alternate baits. It also took less time to
remove 50% of the baits during fat/meat trials (46.7±10.4
sec, 2 fat; 8 meat) than fat/cracker trials (83.3±53.0 sec,
5 fat; 5 crackers), though this difference is non-significant.
There were individual differences in feeding strategies and
bait preferences, indicated by the relative numbers of fats
to alternates taken, the number of fat baits manipulated,
and handling times in each condition (Table 11).

Table 11. Bait choices of three known Gray Jays when a preferred food was wedged into grooves in a picnic table to increase handling time. Figures are averages for eight trials in each alternate bait condition.

A. Meat Baits as Alternates

Bird	Alternates Taken	Fat Baits Taken	Fat Baits Attempted	Handling Time(sec)	Efficiency(kcal/min)
U	2.5	1.0	4.1	55.0 ± 15.3	4.0 ± 1.1
B	2.5	3.5	10.0	50.0 ± 10.6	9.5 ± 2.6
R	5.0	0.5	1.0	35.0 ± 9.0	6.5 ± 3.0
$\bar{X}$/Trial 10.0		5.0	15.1	Grand $\bar{X}=46.7 \pm 10.6$	6.7 ± 2.7

B. Crackers as Alternates

Bird	Alternates Taken	Fat Baits Taken	Fat Baits Attempted	Handling Time(sec)	Efficiency(kcal/min)
U	4.0	0.5	2.0	25.0 ± 19.0	5.1 ± 0.9
B	3.1	5.8	15.2	150.0 ± 46.5	9.6 ± 2.3
R	2.9	3.2	8.1	75.0 ± 49.1	8.7 ± 1.0
$\bar{X}$/Trial 10.0		9.5	25.3	Grand $\bar{X}=83.3 \pm 53.0$	7.8 ± 2.4

DISCUSSION

A comparison using only three birds undoubtedly affects the generality of the statistical analysis. Differences in mean handling times are more indicative of the jay's reaction to wedged fat and alternate baits. When handling time for fat was increased, the birds switched readily to meat but were reluctant to take crackers. In baseline trials, fat was taken twice as often as meat and nine times more often than crackers. In the present experiment, both alternates were taken more often as a result of increased handling time for fat baits. Reluctance to switch to crackers may represent an efficient strategy. Owing to the increased handling time, the profitability of fat baits, E/T, was lowered, and was probably similar to that of meat, as more than one meat bait could be taken per trip. Crackers, which could only be removed singly, remained lowest in profitability and were not accepted as readily.

Other factors besides handling time may have influenced the jays' food choices.

The energy required to obtain a fat bait was calculated to be 0.03 kcal (see Utter 1971), which seems negligible compared to the yield from this food. A great deal of concentration was required to obtain a wedged fat; such activity

competes with vigilance and could leave an animal vulnerable to predation. Anti-predator factors are presumably of considerable importance in the jays' feeding strategy (see Experiment 9).

Bird U switched readily to both alternates and made few attempts to extract fats, often not returning to the table after alternates had been depleted. Bird B was least likely to switch, whereas the bait choices of Bird R were undoubtedly influenced by its strong preference for meat (see Experiment 5). When meat baits were available, Bird R took them almost exclusively and was reluctant to try to take fat, and poor at obtaining them when it did make the attempt. At one point it made 11 consecutive unsuccessful attempts. There was probably a motivational component in this bird's success at extracting fat baits when crackers were the alternates, as successful attempts increased to 38% from 10%, when meat was available. While not ignoring individual differences, overall there was a greater readiness to switch to meat than to crackers when the handling time for fat was increased.

EXPERIMENT 8

The Effect of Mimicry on Food Choice.

Recognition time is another cost that may influence an animal's foraging strategy. Many predators encounter a vast number of potential prey that must be detected and discriminated from non-prey. Predators attend to various characteristics of their prey, such as size, colour, pattern and movement (Curio 1976), and it is unlikely that one cue alone is sufficient to allow correct discrimination. For instance, Kettlewell (1955) found that movement alone does not consistently result in prey recognition by some avian insectivores. Like camouflage, mimicry is a widespread antipredator strategy involving morphological and behavioural similarity between two species in which the noxious taste of one enhances a predator's avoidance of the other (Brower 1969).

In the present experiment, highly preferred fat baits were offered with inedible mimics at equal frequency. It was anticipated that if the presence of these mimics lowered the profitability of the fat, the jays should switch to alternates.

METHODS

Two unmarked, adult Gray Jays were tested on a 2 m^2

area of level, unpaved road. Foods were the same as those
used previously. Styrofoam chips were used as mimics to
increase recognition time for fat baits. To eliminate nor-
mal prey recognition cues, mimics were equivalent to fats
in size, shape and colour, and rubbed with fat to eliminate
potential olfactory differences.

In each of 16 trials, five fat and five mimics were
offered with 10 alternates. On half the trials meat baits
were available, while crackers were offered on the others.
Trials were randomized throughout the experiment with re-
gard to alternate baits, and ended when all natural baits
had been taken, or 10 min after the first jay landed within
10 cm of a bait. Analysis of the first eight baits taken
each trial represents approximately 50%, since five baits
were inedible mimics. This also caused the expected ratio
of alternates to fats to be 2:1 rather than 1:1. Total de-
pletion times were also measured.

RESULTS

The jays switched readily to meat baits but persisted
in choosing fat over crackers (Table 12). They frequently
manipulated mimics in both conditions, but did so signifi-
cantly more frequently when crackers were the alternates.

The more persistent testing of fat baits when crackers

Table 12. Results of bait mimicry experiment in which Gray Jays were offered fat baits; inedible mimics and an alternate food. Replicate of eight trials in each alternate food condition.

Comparison	Mean	Alternate Food	Wilcoxon T	p ≤
$\bar{X} \pm$ S.D. Total Depletion Time (sec)	388.0±73.5	470.0±56.6	0	0.01
$\bar{X} \pm$ S.D. Number Fat Baits Manipulated	17.5±1.7	27±1.7	0	0.025
$\bar{X} \pm$ S.D. Number Alternates Taken	5.5±0.8	3.4±0.8	1	0.01
$\bar{X} \pm$ S.D. Number Fat Sox Choices in First Sox Choices				
$\bar{X} \pm$ S.D. Alternates Remaining at Time of Fat Bait Depletion	1.1±1.4	6.1±1.4	0	0.01

were available resulted in significantly longer depletion times, compared to trials that offered meat baits. The jays took significantly more meat baits than crackers during their first eight selections.

Selection of meats did not differ significantly from the expected 2:1 ratio ($\underline{X}^2 = 0.13$, df=1, p>0.05), but the jays were persistent in choosing fat over crackers ($\underline{X}^2 = 17.34$, df=1, p<0.01).

DISCUSSION

Continued persistent testing of fat indicated that the jays were deceived throughout the experiment, and that they were probably reluctant to switch to an alternate bait. Conversely, the large number of meats chosen during their first 50% selections was interpreted as an indication that meat was a more preferred alternate than crackers. Increased recognition time for fat baits lowered their profitability, as shown hypothetically by the clock-wise rotation of the E/T line in Figure 13. This interpretation could apply as well to Experiments 4 and 6, in which increased search and handling times, respectively, lowered the value of fat baits.

In the present experiment, the jays were not as willing to spend time and energy to find fat baits when a profitable, easily obtainable alternate was available. The tendency to

Figure 13. Hypothetical relationship between prey
recognition time and profitability, shown by the
clock-wise shift of the E/T line for fat baits. Meat
baits move into the optimal diet because they now have
a higher profitability, while crackers remain lowest
in value. (Adapted from Krebs and Davies 1978).

ENERGY (E) →

fat

meat

THE EFFECT OF
RECOGNITION TIME

crackers

TIME (T) →
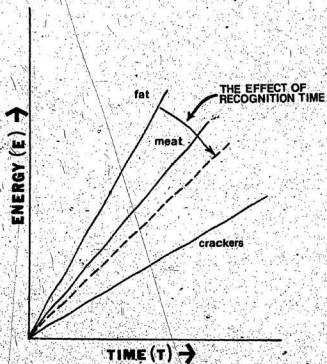
show partial preferences may have been the result of
sampling (Gibb 1960), or simply a need to maintain a
varied diet.

EXPERIMENT 9

Effects of a Predator Model on the Feeding Behaviour of Gray Jays.

Alarm calling, distraction displays and mobbing are three anti-predator defense strategies employed by many avian species (Harvey and Greenwood 1978). Anti-predator behaviour affects patterns of sleep (e.g. Jouvet 1967), activity (e.g. Guggisberg 1972), and nest site selection (see references in Curio 1976). Foraging strategies such as flocking are also thought to be shaped in part by predator pressure (Pulliam 1973). Studies by Powell (1974), Siegfried and Underhill (1975) and others have found that larger flocks often respond sooner to a predator and spend more time feeding than smaller flocks.

Patterns of optimal foraging are also surely shaped by predation pressures as well as the nutritive values of foods, and in the present study the effect of a model Great Horned Owl (Bubo virginianis) on the feeding behaviour of a family of Gray Jays was investigated. It was expected that the presence of a predator decoy would disrupt normal (baseline) feeding responses, particularly in the presence of recently fledged jays, as antipredator responsiveness is most intense in species with altricial young around the time of fledging

(Armstrong 1947.)

METHOD

A family of Gray Jays, comprised of two adults and three fledglings (Figure 14), was offered the three foods used in previous experiments. A 42 cm plastic Great Horned Owl decoy and a 35 cm stuffed, female Ring-necked Duck (Aythya collaris) were presented on random feeding trials. Great Horned Owls breed in Newfoundland, and tests were carried out beside a pond that was frequented by Ring-necked Ducks. Because recently fledged jays had not been tested previously, eight baseline trials were run to determine possible differences in food preference between young and adult birds. Thirty baits, 10 of each type, were randomly spread over approximately 2 m^2 of ground at the start of each trial. The initial 50% of the birds' choices were analyzed.

Twenty-four trials were then run, eight each in the 'owl', 'duck' and 'no decoy' conditions; test conditions were randomized across trials to control for habituation effects of repeated testing. A jay within 7 m of the baits was judged to be in the feeding area, and latency was measured from this time until the first bait was taken. A trial ended when all baits had been removed, or 10 min

Figure 14. A juvenile (top) and adult Gray Jay that were tested in Experiment 9.

after the first bait had been taken. Pilot trials showed
that the owl decoy disrupted feeding responses, and as a
result, depletion times for the first 10 baits were con-
sidered in this portion of the experiment.

RESULTS

During baseline trials, both the juveniles and adults
took 60 baits; however, because three juvenile and two adults
fed, the mean ($\pm$S.D.) number of baits taken/bird in each
age class was 2.6 ± 0.6 and 3.8 ± 0.9 respectively ($t=3.34$, df=
14, $p<0.01$); adults averaging ($\pm$S.D.) 1.7 ± 0.6 baits/trip,
compared to 1.3 ± 0.5 for juveniles ($t=3.78$, df=14, $p<0.01$). Juven-
iles were non-discriminating in selecting baits, taking each
type about equally, whereas adults took mostly fat and meat,
and few crackers (Table 13).

The presence of the owl decoy disrupted the jays feed-
ing responses, whereas the duck decoy did not. Latency to
feed was 123.1 ± 123.9 sec when the owl was in the area, com-
pared to 17.7 ± 12.7 sec and 10.6 ± 5.6 sec in the 'duck' and
'no decoy' conditions, respectively ($F_{2,33}=8.45$, $p<0.01$).
There was no significant difference in latencies between
control conditions.

Adults and juveniles did not react differently to the
owl decoy. There was no significant difference between

Table 13. First 50% bait choices of three juvenile and two adult Gray Jays. Replicate of eight trials. Significant differences (determined by x^2 test of expected equal preference) are indicated.

Age Class	Bait Type			x^2	p
	Fat	Meat	Crackers		
Juveniles	22	19	19	0.30	>0.05
Adults	26	27	7	12.70	<0.01
Totals	48	46	26		

feeding latencies of young and adult jays. Once feeding had
begun, owl trials progressed more slowly than either duck or
no decoy trials. The mean depletion time for owl trials was
375.6± 167.8 sec (two trials had to be terminated after 10
min), and for duck and no decoy trials were 175.6± 38.7 sec
and 141.9± 52.7 sec, respectively. The difference among the
three conditions is significant (F2,21=11.84, p<0.01), and
that between controls is not.

Fewer baits were taken during the owl trials, but the
proportionate selection of the jays did not change across
experimental conditions. Fat and meat baits were consistently
preferred to crackers, but this difference is significant only
in the 'no decoy' condition (x^2=7.69, df=2, p<0.05). Bait
choices of juveniles vs. adults differed from expected in
the owl (x^2=6.57, df=3, p<0.02) and duck decoy conditions
(x^2=18.25, df=3, p<0.01), but not in the no decoy condition.
Juveniles and adults differed in their selection of crackers
in the owl condition (x^2=9.00, df=1, p<0.01), and of crackers
(x^2=5.76, df=1, p<0.02) and fats (x^2=10.80, df=1, p<0.01)
in the duck condition. No difference in meat preference
was found between age classes (Table 14).

There were highly significant negative correlations be-
tween trial number and depletion time (r_{rho} = -0.92) and be-

Table 14. First 50% bait choices of three juvenile and two adult Gray Jays in three experimental conditions. Replicate of eight trials in each condition.

Bait Type	Owl Decoy			Duck Decoy			No Decoy			Total
	Age Class		Sub Total	Age Class		Sub Total	Age Class		Sub Total	
	Juvenile	Adult		Juvenile	Adult		Juvenile	Adult		
Fat	14	14	28	6	24	30	14	19	33	91
Meat	16	8	24	18	11	29	14	18	32	85
Crackers	14	2	16	16	5	21	11	4	15	52
Totals	44	24	68	40	40	80	39	41	80	228

tween trial number and latency to feed (r_{rho} = -0.75) in the owl condition.

DISCUSSION

The high selectivity of adults compared to juveniles may have been the result of prior experience, especially with human foods. Juveniles appeared to land and take baits at random; the data support this observation. Only in later trials did young birds consistently take more than one bait/trip, and the possibility of observational learning must be considered. The combined choices of this group of jays differed slightly from the bait preferences of adult Gray Jays offered the same bait combination (see Table 7, Experiment 6).

During the experiment, adults had a shorter feeding latency than juveniles in the 'no decoy' condition and longer latencies when either decoy was present. The role of prior experience may explain this tendency as well: juveniles, probably without prior experience with avian predators, showed no fear. In general, the young jays were much less wary of the decoy than adults, nor were they wary of me, often approaching to within an armlength. Increased juvenile latencies, though not significant, seem to result from adult alarm calling.

Depletion times, which reflect fearfulness and caution, were considerably longer during owl trials. Once initial fear had been overcome, the jays were still extremely wary and continued to fly from tree to tree before returning to the baits. No such behaviour was observed during duck trials, so it was the presence of the owl, and not simply another bird, that evoked alarm responses in the adult jays. Anti-predator behaviour attenuated over trials, probably due to habituation to the owl decoy. Andrews (1961) found a similar effect in the alarm calling of Blackbirds (Turdus merula) after repeated exposure to an owl decoy.

GENERAL DISCUSSION

In the context of the present series of experiments, the feeding behaviour of these corvids concurs with some basic notions of optimal diet, optimal allocation of time for feeding, and food selection in terms of its net energy value. In light of the fact that these birds must rely to some extent on an unpredictable or seasonal food supply in parks and seabird colonies, these findings make good sense. Other predictions, such as an all-or-none type of selectivity with increased food abundance, were not supported by data.

The cost/benefit analysis of raven predation indicated that these corvids fed in an efficient manner, obtaining sufficient energy to meet daily requirements. To compare natural predation with opportunistic scavenging, crows and jays were tested in a series of field experiments in which both species demonstrated patterns of optimal foraging. Increases in absolute and relative abundances of profitable prey led to increased selectivity, as had been widely shown in earlier studies. It was unclear whether the birds had actually become more selective when the frequency of large baits increased or had been non-selective, merely taking common baits. A follow-up experiment showed that there was strong selection against oddity, which indicated that corvids

behave like other predatory birds.

In general, the jays chose baits in terms of net energy value, though some exceptions were found. A cost/benefit analysis of the jays' bait selections showed that these birds used an optimal strategy, although a range of bait preferences, foraging techniques, efforts and efficiencies was found among the three known jays. This type of analysis using a greater number of birds would undoubtedly have produced a wider range of food preferences and efficiencies; however, the present study was constrained by the number of jays I could attract to the park.

Switching, another optimal strategy, was demonstrated in three experiments that increased search, handling and recognition times, respectively, for fat baits. The jays' switch to meat, but their reluctance to take crackers was explained in terms of the relative profitabilities of the three foods, though it is also possible that they preferred meat to crackers, or that crackers did not lend themselves to caching as well as meat. Unfortunately, I was unable to locate the jays' food caches.

While seasonal differences in food preference were not found, age differences were evident, adults being more discriminating than juveniles. The role of learning and the

ontogeny of food choice are two obvious extensions of this
study. Age differences in anti-predator behaviour, while
slightly tangential to the focus of the present study,
raised a sufficient number of questions regarding the roles
of learning and prior experience on which an entire thesis
could be based.

This set of experiments is merely the tip of the ice-
berg: much remains to be done. The social dynamics of Gray
Jay families needs to be studied in greater detail; inter-
action among the three known jays as they selected baits was
particularly interesting, and by isolating and testing cap-
tive birds, actual food preferences, without the influence
of intraspecific competition, can be readily determined.

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APPENDIX A

Physiological and Behavioural Adaptations of some Temperate Area Corvids, and Their Relation to Feeding and Non-Migratory Existence.

The Corvidae is a diverse group of passerine birds with more than 100 species that are subdivided into the typical crows, jays, and magpies, as well as smaller groups such as the choughs and nutcrackers (Goodwin 1976). Most species nest in trees, but adaptation to cliffs and other treeless habitats is common, and at least one species, Hume's Ground Jay (Pseudopodacus humilus) digs out a nest cavity in an earthen bank (Ali in Goodwin 1976).

Except for ground jays, corvid plumage tends to be ornate, with little selection for crypsis. Plumage or immature birds resembles that of adults, but where marked differences occur, a high degree of sociality is often found. This may serve to reduce aggression during times of limited food supply (Goodwin 1976). Conspicuous differences between juvenile and adult plumage are found in jays of the genus Perisoreus.

Size and shape of corvid bills are usually correlated with feeding method or food type. Members of the genus Corvus, the most omnivorous of the family, tend to possess

strong, slightly hooked bills which reflect their broad
feeding habits. Strong, pointed bills of the nutcrackers
are probably an adaptation to feeding on cone seeds (Amadon
1944), while the decurved bills of choughs and ground jays
apparently aid in their probing search for food (Goodwin
1976).

Corvids are an enormously successful family and lack
representation only in New Zealand and Polynesia (Goodwin
1976). Some members such as the Common Raven, (_Corvus
corax_), maintain a holarctic distribution (Coombes 1978). Their
aggressiveness and opportunistic feeding strategy have en-
abled corvids to outcompete many other species. Although
the raven's ability as a predator is well documented (e.g.
Aspden 1928; Tinbergen _et al_. 1962; Montevecchi 1979), it
is truly omnivorous. Bolan (cited in Coombes 1978), analyzing
the faecal castings of ravens, found 16 different food types,
including animal matter, seashore objects, seeds and insects.
The diets of crows are equally diverse (e.g. Butler 1974;
Burger and Hahn 1977). Jays and nutcrackers are somewhat
more specialized in their diets, which consist largely of
acorns and pine seeds, respectively (Turcek and Kelso 1968).

Corvids are of tropical origin (Amadon 1944) and the
majority of modern forms live in tropical and subtropical

areas. Temperate woodlands, which in winter bear no fruit and harbour few insects, support those corvid species that have become adept at finding food and utilizing energy efficiently. It is in this small proportion of corvids that occupy boreal-alpine and sub-arctic zones that caching, or food storage, has evolved to the greatest degree (Turcek and Kelso 1968). Caching is also widespread among the Paridae and some woodpeckers (Curio 1976), and the fact that all these species are largely found in temperate and sub-arctic zones suggests a climatic basis for food storage. Within the Corvidae, food storage is most common in the jays and nutcrackers (Coombes 1978). Haftorn (1956) estimates that up to 60% of the food eaten by Blue Jays (*Cyanocitta cristata*) in winter is obtained from caches. This same level of dependence on caches has been found for Great Tits (*Parus major*; Gibb 1960). Mezhanni (cited in Turcek and Kelso 1968) calculated the number of caches made by the Nutcracker (*Nucifraga caryocatactes*) in a year to be 6,000, which would contain 70,000 seeds and weigh 4-5 kg. Reimers (1959) found a 6-33% range in recovery success by nutcrackers, whereas Turcek (1966) estimates that 70% of caches are recovered. Jays may be better at recovering cached food. Richards (1958) observed an 88% success rate by the European

Jay (Garrulus glandarius) for recovery of cached acorns
through 45 cm of snow; even in 85 cm of snow these birds
go directly to their stores (Dulkeit 1960). Bossema (1968)
found that European Jays recover hidden acorns by locating
oak saplings that have begun to grow up from the ground.

Jays and nutcrackers have evolved two types of morpho-
logical adaptations for food transport and storage. The
enlarged sublingual pouch in the nutcrackers and Old World
jays enables them to carry large numbers of seeds and
acorns, respectively. Nutcrackers can transport up to 200
seeds (Turcek and Kelso 1968), and jays carry as many as
nine acorns (Bossema 1968; see also Chettleburgh 1952).
An enlarged salivary gland in the Gray Jays (Perisoreus
spp.) enables them to encase food in a sticky secretion
that adheres readily to forks in branches, crevices in the
bark, and lichens hanging in trees (Bock 1961). These plugs,
or boli, harden creating discrete packets of food which the
jays recover during winter. Dow (1965) found intact boli
which had been deposited three months earlier, though it is
likely a stored bolus may be useful to the jays for longer
periods.

The Gray Jays

Gray Jays occur widely in the Old and New Worlds and

include the Siberian Jay (Perisoreus infaustus) and Sooty
Jay (P. internigrans) of northern Eurasian forests, and
the American Gray Jays (P. canadensis) of coniferous
forests from Newfoundland to Alaska (Goodwin 1976). The
Gray Jay is non-migratory throughout its range, though
local movements of 7.5-15 km have been noted for the Siberian
Jay (Lindgren cited in Coombes 1978). Breeding occurs early,
often while snow still covers the ground. Warren (1899)
observed nest-building by jays in Michigan on 22 February;
egg dates for this nest were 14-18 March, and hatching was
completed by 4 April. This author also cites records of 17
Newfoundland nests with eggs from 4-30 April. Thus, the
reproductive cycle is completed before competition from
migratory species becomes great, and allows the jays oppor-
tunity to prey on other breeding species (Samuels cited in
Bent 1946). Family groups dissolve at the start of winter,
when jays are commonly found singly or in pairs (Lawrence
1973). Gray Jays pair for life, but will remate should a
partner die (Lawrence 1973).

Jays are omnivorous and prey on a variety of insects
and small mammals, as well as buds and needles of trees and
birds' eggs. A scavenger, this bird is as common at dumps
as crows and ravens (Aldrich 1943). Because of its close

association with man, many human foods comprise a large
portion of the jay's diet.

Determinants of a species' distribution

Kendeigh (1969, p. 441) states "The ability of a
species to metabolize energy under different environmental
conditions may greatly affect its response and behavior,
as shown by the limits it can extend its distribution, the
size and fluctuation of its population in any area, whether
or not it is a permanent resident, the time it initiates
migration, nesting and moult, the size of egg clutches, etc."
Ambient temperature is probably the most important environ-
mental factor which shapes an animal's energy balance and
therefore limits its breeding distribution (Cox in Vechte
1964). Winter temperatures encountered by Gray Jays may
reach -65° C (Scholander et al. 1950), though this bird
maintains a year round body temperature of 41.3° C (Ken-
deigh 1969). Behavioural adaptations such as huddling and
seeking shelter minimize heat loss, but it is insulation
against the cold that enables animals to survive harsh
northern winters. A coefficient of insulation is derivable
from the equation I= TC/E; where I is the coefficient; TC
is the temperature gradient in °C; and E is basal metabolic
rate (BMR) in °C/kcal/m^2/hr (Misch 1960). The Gray Jay
(mass=64 g) has a coefficient of 0.84 and is the most well
insulated of any bird so examined (Scholander et al. 1950).

In comparison, the Snow Bunting (_Plectophenax nivalis_; average mass=40 g), another northern resident, has a co-efficient of 0.48 (Scholander _et al_. 1950), whereas the Ortolan Bunting (_Emberiza hortulana_; average mass=12 g), a migratory species, has a coefficient of only 0.20 (Wallgren 1954).

Heppner (1970) suggests that the black plumage found among _Corvus_ species may be an adaptation to absorb maximum solar radiation, and has demonstrated that a black bird absorbs 3.1 cal/min more energy than a white one the same size. Increased solar radiation has been found to reduce foraging time in White-crowned Sparrows (_Zonotrichia leucophrys_), presumably by providing another source of exogenous energy (Morton 1967).

Periodic weight gain is a basic response to cold shown by non-migratory species; e.g. in Redwinged Blackbirds (_Agelaius phoeniceus_) total fat reserves increase from 1.3% of body weight in summer to 40.3% by winter (Brenner 1967). Baldwin and Kendigh (1938) determined that the major components of weight increase are fat and glycogen, which supply extra metabolic fuel as well as a layer of insulation. Periodic weight gain has survival value: at low ambient temperatures heavier birds live longer than lighter ones

(Kendeigh 1934). However, excess weight gain would be
maladaptive if it increased the likelihood of predation or
costs of locomotion and maintenance (Helms 1968).

King (1972) has shown that fat reserves usually
supply only enough energy to enable a bird to survive over-
night and to begin foraging the following morning. He em-
phasizes that the different strategies to winter survival
taken by animals undoubtedly affects the importance of fat
reserves. Overnight storage of food in the crop by some
birds (e.g. Willow Ptarmigan, _Lagopus lagopus_) may substitute
for lipid storage (Irving, West and Peyton 1967; West and
Meng 1968). Caching, previously mentioned, is yet another
adaptation to a non-migratory existence.

In summary, it can be seen that through physiological
adaptations such as enlarged salivary glands and sublingual
pouches, efficient body insulation, and perhaps black plum-
age, as well as behavioural adaptations that include caching
and omnivorous feeding habits, many corvids have become non-
migratory in temperate regions with severe winter conditions.
Feeding and foraging behaviour, which are the subject of the
present thesis, also represent important adaptations for
corvid existence in temperate zones.