Foraging Behaviour in Bullfinches (*Pyrrhula pyrrhula*).

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Abstract

The foraging behaviour of bullfinches (*Pyrrhula pyrrhula*) was investigated in the field and in the laboratory. Their ecology as a pest of fruit orchards is discussed with reference to data on their movements and feeding habits obtained through radiotelemetry. Bullfinches spend most of their time within home ranges occupying less than 5 ha. Damage to fruit buds is most likely to be caused by resident birds. Laboratory studies examined the birds' abilities to assess the prospective profitability of seeds by using proximate cues such as size and shape; and their efficiency at tracking changes in the quality of food patches. A model was developed which predicts the conditions under which birds should prefer variable over constant food sources. It is argued that animals will generally avoid patches where food arrives in variable amounts, but should prefer patches where food arrives with variable delays. When amount and delay are both varied, then the preference will depend on an animal's current feeding rate in relation to that required to meet its necessary energy budget. The model also simulates the behaviour of birds foraging in an environment of depleting patches and can explain a number of seemingly sub-optimal foraging strategies discussed in the operant psychology literature. It is suggested that cognition may play an important role in animals which can adapt their foraging strategies to suit changing conditions. Evidence is presented that hooded crows (*Corvus corone cornix*) are able to grasp the nature of simple causal relationships and make use of this knowledge in new situations. The conclusion is a qualified defence of optimal foraging theory.

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Introduction

The experiments and ideas described in this thesis are loosely connected by two things -- bullfinches and optimal foraging theory. "Loosely," because bullfinches do not appear in every chapter and neither does optimal foraging theory.

Bullfinches are pests of fruit orchards. By studying how they forage in the field and in the laboratory it was hoped to discover some of the influences on their choices of where and what to eat. The more that is known about how bullfinches make such decisions, the better the prospects of manipulating their behaviour.

Optimal foraging theory assumes that animals have evolved to make the most of the environments in which they find themselves. In evolutionary terms, "making the most" of something means maximising reproductive fitness. In terms of foraging theory, maximising reproductive fitness has generally been equated with maximising rate of energy gain. Several of the experiments described here evaluate bullfinches' success in acheiving the best possible feeding rate. More sophisticated theories are now looking at how birds may maximise more general functions, such as the probability of surviving a winter's night. Such theories predict that animals will be sensitive not only to the average feeding rate but to its variance. This is the subject of chapter 4.

Each chapter is more or less self-contained, having its own introduction and conclusion. Hence this general introduction will do little more than elaborate the list of contents.

Chapter 1 describes the natural history of bullfinches feeding on fruitbuds in a Kent pear orchard. Recent advances in radiotelemetry technology have enabled the manufacture of transmitters light enough to be carried by birds as small as bullfinches. In this way the movements and feeding activities of known individuals could be monitored in the field.

Chapter 2 investigates bullfinches' abilities to use the size and shape of seeds as guides to the time needed to dehusk them, the probability of dropping them during handling, and the size of the kernel inside.

Chapter 3 looks at birds' abilities to track changes in the quality of different food patches, It attempts to discover what cues they use in doing so, and whether they are influenced by previous experience.

Chapter 4 presents a general model of foraging behaviour. It attempts to provide a common causal explanation of a number of apparently contradictory observations in the literature. In particular, it predicts the conditions under which animals should prefer variable over constant food sources, and the kind of variability they should prefer. The model is shown to perform efficiently in an environment of depleting patches. (An earlier version of this thesis described empirical evidence that risk sensitive behaviour in bullfinches is better explained by the model than by strictly functional arguments. On the instructions of my examiners, that chapter has been omitted.)

Chapter 5 is about possible cognitive mechanisms underlying foraging behaviour and describes an experiment using hooded crows (*Corvus corone cornix*). The results suggest that they are able to appreciate simple causal relationships and make use of this knowledge in new situations.

The conclusion discusses the usefulnesss of applying functional models to foraging behaviour.

Chapter 1

Natural history and home range

1. NATURAL HISTORY

1.a. Pest Status

Damage to fruit trees by bullfinches has been recorded since the 17th century (Wright and Summers, 1960). In the reign of Elizabeth I a bounty of a penny a head was offered for every dead bullfinch. Today, the Ministry of Agriculture, Fisheries and Food recognises the birds as an economic pest of fruit orchards and permits growers to shoot and trap them. Bullfinches eat the flower buds of a wide range of cultivated fruit trees; most notably the buds of apples, pears, plums, cherries, gooseberries and currants. Being rather shy birds, most of the damage is concentrated along the edges of orchards, close to cover. A typical bird can consume 30 gooseberry buds in a minute, or two bushes in an hour (Wright and Summers, 1960). Newton (1964) counted bullfinches eating hawthorn buds at the rate of 30 a minute, and pear buds at 25 a minute. I have watched a male bullfinch feed in a hawthorn tree at a similar rate, for a full hour. Matthews and Flegg (1981) reckon that a single bird is capable of stripping two to three full-size pear trees a day. They estimate that in the winter of 1978 one 2 ha pear orchard in Kent lost 1.2 million fruit buds to bullfinches (Flegg and Matthews, 1979). In other words, a few bullfinches can eat a lot of buds.

The effects of bud-eating are most noticeable in springtime. While trees in the centre of an orchard are covered with blossom, those at the edge may have lost nearly all their flowers. The contrast is often dramatic (see plate 1). However, the degree of damage is very variable and the birds much prefer certain cultivars to others.

Farmers may have overestimated the degree of economic injury caused by bullfinches. Wright and Summers (1960) found that pear trees which had lost as many as 70% of their buds did not produce a significantly smaller crop. Summers (1982) simulated bullfinch damage by removing known proportions of buds from Conference pear trees. At levels of 30 and 40% bud loss, he estimated that the reduction in yield was 0.68% of the total, or £37 per hectare (1976 prices). Only when trees were severely denuded in

Plate 1.



A pear orchard in blossom. Damage is greatest along the edge nearest to cover.

successive years did yields decline significantly. In addition, trees compensated for damage in the previous year by producing heavier crops the following year, in comparison with undamaged trees. Similarly, Matthews (1983) has argued that moderate grazing of Conference buds by bullfinches can be beneficial to the fruit grower. Bullfinch damage was high in 1978 and he estimated the financial loss per hectare at £1291. In 1979, when damage was light, losses amounted to only £128/ha and in 1980 there was a gain in yield, compared with controls, worth £253/ha.

If bullfinches could be persuaded to avoid the outer rows of an orchard (where damage is heaviest) and/or to spread their feeding more evenly through the orchard or to feed on something else (such as weed seeds, ash keys or hawthorn buds) then they would no longer be a pest.

Measures to limit the damage done by bullfinches would be more effective if it were known when the birds were most likely to strike (bud loss varies enormously from year to year); how many birds are responsible and how far they travel (trapping and shooting work better against small numbers of local residents); which features of the fruit buds best explain the birds' preferences for particular varieties (is it differences in their shape and size (Summers and Huson, 1984) or their chemical constituents (Greig-Smith et al., 1983, in preparation)?). An understanding of these characteristics may enable farmers to lessen damage by planting less-preferred varieties around the orchard margins; it could encourage breeders to select resistant varieties; or it could be the first step in the formulation of a repellent spray.

1.b. The Ecology of Bud-feeding

1.b.i. The timing of bud-feeding

Hawthorn (*Crataegus monogyna*) and blackthorn (*Prunus spinosa*) are the most common natural source of buds for bullfinches; buds of wild cherry (*Prunus avium*), aspen (*Populus tremula*), birch (*Betula* spp.), wych-elm (*Ulmus glabra*) and larch (*Larix decidua*) may also be taken when available. They are eaten, mainly between January and April, and cultivated fruit trees also suffer most damage at this time. The precise onset of bud-feeding is variable, and may depend on the availability of other foods such as the seeds of dock (*Rumex* spp.), bramble (*Rubus fruticosus*), nettle (*Urtica dioica*), ash (*Fraxinus excelsior*), birch (*Betula* spp.) or privet

(*Ligustrum vulgare*). The developmental stage of the buds may also influence the timing of bud-feeding and the bullfinches' preferences.

Newton (1964) mounted the first detailed study of the ecology of bullfinch bud-feeding. It was conducted over three years in Marley wood, Oxfordshire. He found that bullfinches were most likely to attack fruit trees when the abundance of weed and tree seeds was low. Damage was particularly severe in the winter of 1961/62 when bramble seeds and ash keys ran out by January. During this period it seems that trees were synchronously producing ash keys every second year. In the south of england, ash mast was high in 1958, 1960 and 1962. Fruit-growers reported that bud loss was greatest in the intervening years.

If birds resort to eating buds only when weed and tree seeds are scarce, then perhaps fruit-growers should do their best to ensure that seeds do not become scarce; they could plant ash trees for example. The main problem with this approach is that a plentiful supply of ash keys might allow vulnerable birds, which would otherwise die, to survive the winter and swell population numbers in following years. If, for any reason, the seed supplies failed to meet demand, there would be an unusually large population of bullfinches ready to descend upon fruit trees with potentially disastrous results for growers. Matthews and Flegg (1981) propose a way around the problem. They suggest that growers refrain from spraying orchard floors with herbicides, and rather, encourage the growth of nettles and docks. Growers could net these plants until the winter has killed off the weaker birds, and uncover them before serious bud damage is underway.

Support for the link between bud-feeding and the scarcity of ash keys comes from Summers (1981). A negative correlation was established between the percentage of bullfinch guts containing ash keys and the amount of damage done to Conference trees, for the years 1969-1975. However this relationship was significant only for January of each year. Furthermore, there was a significant positive correlation between the presence of weed seeds in guts and damage to Conference buds. This contradicts Newton (1964) and casts doubt on the efficacy of Matthews and Flegg's proposal that growers should spare docks and nettles in the hope that bullfinches will find them more attractive than fruit-buds.

Buds are a poor food source compared with seeds. Ash keys have a high calorific value and are rich in fat and protein (Table 1, see also Matthews, 1983) whereas buds, being 50% water in January, supply little

fat, protein or carbohydrate. While there are any ash keys or seeds of any sort left, it is puzzling that bullfinches include buds in their diet at all. Yet Flegg and Matthews (1979, 1980) recorded substantial damage in three consecutive winters even though there was no shortage of ash seeds. Three series of experiments (Newton, 1964; Summers, 1982; Matthews and Flegg, 1981) in which captive birds have been fed solely on pear buds in January (as many as 400 an hour) have shown that they invariably lose weight. As spring approaches and the buds swell, they become more profitable and body-weights of birds on a bud diet are maintained. The

Table 1. Chemical analyses of buds and seeds eaten by bullfinches during winter. (From Greig-Smith and Wilson, unpublished data)

Food Type	Date	Soluble Protein	Free Amino Acid	Glyceride Glycerol	Starch	Glucose	Fructose	Sucrose	Phosphorous
				(mg/g dry weight)					
Buds									
Hawthorn	Feb 12	4,0		20,0	1,3	16,8	10,0	2,0	3,0
Aspen	Feb 12	5,5	3,9	41,7	0,0	30,8	22,9	0,4	3,8
	Mar 9	4,6	8,7	34,5	19,0	44,4	21,6	0,0	3,9
Conference	Feb 12	1,5	2,6	21,7	0,0	39,7	23,1	0,0	3,9
Comice	Feb 12	0,6	1,1	35,2	1,7	40,5	21,5	0,0	5,1
Seeds									
Bramble	Feb 12	0,7	0,8	32,5	5,3	1,8	0,9	0,4	1,9
Dock	Feb 12	2,3	1,3	12,7	39,1	3,0	2,8	0,9	3,4
	Feb 26	4,2	1,7	9,1	52,9	1,8	1,4	1,3	2,7
Ash	Feb 12	74,0	2,7	143,7		9,2	3,5	1,5	2,4

rate of bud swell is partly dependent on average winter temperature. The colder the winter, the slower the buds grow. Matthews and Flegg suggest that, "contrary to popular belief, cold weather in late autumn and early winter might delay rather than promote damage."

In general, it seems that birds lose more weight when fed hawthorn buds than pear buds, and lose more weight on a diet of Comice than Conference buds. (Conference trees suffer more attacks from bullfinches in orchards than do Comice trees.) Matthews and Flegg recorded no weight loss when birds were fed bramble seeds or a mixture of dock and ash keys, although the birds did lose weight on a diet consisting only of dock

seeds. Newton (1964) noted that bullfinches kept on a diet of hawthorn buds in January spent more than 90% of daylight hours engaged in feeding; the equivalent figure for pear buds was 75%, while birds kept on a proprietary mixture of bird seed spent only 24% of the day feeding.

Possibly, buds contain small amounts of some essential nutrient. Cage-bird fanciers often include greenery in the spring diet of bullfinches in the belief that this improves their breeding condition. Matthews (1983) tested this hypothesis by feeding 3 male birds a total of 15000-45000 Conference buds between February and March. Compared with three control males, who were not given buds to eat, there was no difference in rate of testis growth.

1.b.ii. Food preferences: ash keys

Newton (1967) noted that bullfinches favoured particular ash trees, returning to them year after year and virtually ignoring the keys of nearby unfavoured trees. Matthews (1983) and Greig-Smith and Wilson (1985) have also demonstrated preferences, between ash trees. This may help to explain why bullfinches will eat buds, even though nutritionally rich ash keys are still available. The ash keys left may be unsuitable, being too difficult to handle or containing too-high concentrations of toxic or distasteful chemicals.

Ash keys come in a range of sizes, both within and between trees, and this is likely to affect their ease of handling. If certain trees have keys which are especially difficult to split and eat, then birds should pass them by. Similarly, within a tree, resistant keys may be rejected in favour of more wieldy ones. It has been noted (Matthews, 1983; Greig-Smith and Wilson, 1985) that bullfinches drop, deliberately or accidentally, as many as half of the keys they pluck.

From casual observations in the field, it seemed to Matthews (1983) that bullfinches chose not to feed in ash trees with very large keys, presumably because large keys take longer to crack open and to eat. He found that captive birds allowed to choose between bunches of keys from different trees, distinctly preferred bunches of small keys (average weight 31.0 mg). In an experiment where 16 birds were fed only large keys (45.1 mg), all but one bird lost weight, and after three days, five birds had died. However, as the keys in a particular bunch all came from the same tree and as a detailed record of handling times was not made, it is difficult to prove that the birds preferred smaller keys because they were

quicker to eat, or because they tasted nicer or were more digestible or for some other reason. When Matthews made a more rigorous attempt to correlate the preferred trees of wild birds with ash key size, he found no significant relationship. Greig-Smith and Wilson (1985) could find no significant relationship between the handling times of birds observed feeding in a particular tree and the average key weight for that tree. Mackenzie (1983) also failed to establish a connection between key length or weight and handling time for captive birds. It seems unlikely that birds choose to feed in a particular tree simply because it has small keys with short handling times.

Greig-Smith and Wilson were more successful in linking preferences with the contents of ash keys. They found that birds preferred those seeds in which the rate of fat intake was high, while the amount of phenolic compounds ingested was low. Polyphenols, in the form of tannins, are known to interfere with the digestion of proteins by herbivores and they are believed to act as a chemical defence in many plants. The rate of protein intake had little influence on the birds' preferences. The size of ash key seemed to affect preferences insofar as it contributed to the rate at which phenolic compounds were being ingested. The *concentration* of phenols did not correlate with preference. However, a difference was discovered between trees which lost their keys early on (to bullfinches or through natural dropping) and those which retained their keys throughout the winter; the latter had a higher concentration of phenols. The longer that ash keys remain on the tree, the drier and more indigestible they become (Matthews, 1983). Even in August, when they are still green, the keys are less digestible than canary seed (83% compared with 94%). By May they are only 65% digestible, which is close to the digestibility of the outer leaves of pear buds, and bullfinches usually discard these leaves.

An apparent abundance of ash keys in midwinter is not proof that bullfinches have an adequate food supply. Buds, poor as they are, may be a more profitable alternative.

1.b.iii. Food preferences: buds

We have already noted that, of the two most commonly grown pear varieties, bullfinches prefer the fruit buds of Conference to Comice trees. In captivity, they also maintain weight for longer on Conference than on Comice than on hawthorn buds. According to Newton (1964) and Summers

(1982), birds feeding on hawthorn buds take the largest ones first, removing the outer scales and eating the central flower initials. Hawthorn and blackthorn flower initials weigh 0.5-2 mg (dry weight) in January and February. Cultivated fruit buds are larger (3-9 mg dry weight) and begin to swell earlier than wild varieties: and Conference initials weigh about 3 mg more and begin to expand sooner than the less-preferred Comice buds. Newton suggests that bullfinches can eat large buds nearly as quickly as small ones and that therefore they may be expected to prefer cultivated buds. Matthews and Flegg (1981) however, argue that bullfinches can compensate for the smaller size of hawthorn and blackthorn buds by eating them faster. Summers (1982) using captive bullfinches, found that they ate similar numbers of Conference and Comice buds, that there was no significant difference in the calorific content per gram between the varieties, and yet birds obtained significantly more calories per day from Conference than Comice buds, because of the difference in size.

Summers and Huson (1984) measured the size and shape of a variety of pear cultivars in an attempt to predict their susceptibility to bullfinch attack. From their history of bullfinch damage over three years, thirty six cultivars were classified as favoured or unfavoured. A linear discriminant analysis was performed on bud shape of 15 varieties in 1978. Bullfinches preferred buds which were short and whose edible core was large in relation to the volume of outer husk or bud scales. When this discriminant function was applied to data on 32 varieties measured in 1982, it correctly classified all but three cultivars as favoured or unfavoured. These results underline the importance of being precise about what is meant by "size". If size is equated with length, then bullfinches could be said to prefer smaller sized pear buds. Furthermore, relative bud length is not especially consistent between years. From Summers and Huson's data for 11 varieties whose bud lengths were measured in both 1978 and 1982, the correlation between years was only just significant ($r=0.55$, $p<0.05$, 1-tail). (The correlation for core volume/husk volume ratio was better with $r=0.70$, $p<0.01$, 1-tail.)

Summers and Huson's results suggest that bullfinches' preferences between different pear cultivars are based on the physical characteristics of the buds, in particular, the relative volume of the edible core. They also present evidence that favoured varieties are easier to pluck from the branch than less popular varieties. This fits in well with optimal foraging theory which predicts that feeding animals should try to improve

their rate of intake, by choosing food items that provide as much energy in as short a handling time as possible.

As we have seen with ash keys, birds may value other qualities besides energy content. The amount of proteins or toxins, for example, may be important. Summers and Jones (1976) found that varieties of pear buds with a high percentage of nitrogen were especially vulnerable to attack by bullfinches. A more detailed chemical analysis by Greig-Smith, Wilson, Blunden and Wilson (1983) showed that Conference buds contain a significantly greater concentration of free amino acids and fructose than Comice buds. Wilson and Blunden (1983), and Wilson (1984) have shown that Conference buds have a greater total phenolic content yet less protein-precipitating polyphenols than have Comice buds. The latter substances are known to taste astringent and may interfere with protein digestion. Clearly bullfinches may prefer Conference buds for a variety of reasons.

Greig-Smith (1985b) investigated the ability of bullfinches to distinguish between cultivars using only flavour cues. Hemp seeds (*Cannabis sativa*), a favourite food of captive bullfinches, were coated with extracts of Conference and Comice buds, and one or other flavour was presented to the birds, in conjunction with a separate dish of control seeds which had been coated merely with acetone. Birds ate as many of the flavoured seeds as control seeds, but subtle behavioural differences were observed in the course of feeding. First visits to dishes of flavoured seeds were shorter and the number of pecks made were fewer than first visits to the control dish. Birds were more likely to take a drink after eating Comice flavoured seeds. Husking times were shorter for flavoured seeds than for control seeds, suggesting that the birds were minimising their contact with them. Birds were also far more likely to drop flavoured seeds. Differences were slightly more pronounced when Comice flavour was used. These results suggest that the birds found flavoured seeds distasteful and that Comice flavour was more distasteful than Conference flavour.

Greig-Smith and Wilson (in preparation) have conducted a more sophisticated study of bullfinch flavour preferences using extracts from 30 pear cultivars. Seven behaviours were measured and entered into a principal components analysis. Three factors emerged, explaining 79% of the variance, which were labelled handling behaviour, seed consumption, and duration of the first feeding bout. The total phenolic content of each of the cultivars was then compared with their weightings on each of the

factors, but no significant correlations emerged. This indicates that preferences between cultivars could not be explained in terms of the quantity of tannins present. However, a more detailed analysis using High Performance Liquid Chromatography, identified 37 assayable phenolic compounds. These were entered into a multiple regression analysis and 13 of them explained 71% of the variance in factor I (handling behaviour) and 90% of factor II (consumption). Not all of the compounds were avoided; some appeared to be attractive. This suggests that the idea that phenolics are generally distasteful to herbivores is an oversimplification.

That bullfinches appear to be sensitive to "natural" flavours in a laboratory environment and in the absence of other cues, suggests that such flavours may play a part in the preferences of wild birds and could be used in the development of feeding repellents.

1.c. Field observations

Bullfinches are often described as shy or skulking birds. They do not defend a territory and it is difficult, even with marked individuals, to keep them in view for very long (Greig-Smith and Wilson, 1984; Newton, 1964). Direct information about bullfinch movements and feeding behaviour has usually been obtained by walking a regular route through the study area and recording bird sightings and calls at scheduled stopping points. Indirect information has been obtained through mark-recapture techniques and through gut content analyses of birds trapped by fruit-growers. In the present study, several birds were fitted with radio-transmitters (see part 2 of this chapter). The position of known individuals could be monitored throughout the day.

In January, February and March of 1983, radio-tagged birds were monitored from dawn till dusk for two days a week. On any given day, one bird was chosen as the focal bird, and its location noted every 5 minutes. Although the observer could keep within 20-30 m of the focal individual without obviously disturbing it, direct sightings were relatively rare. In 220 hours of bird-watching, less than 24 hours of feeding behaviour was observed for nine radio-tagged birds. I hoped to establish whether all birds in a local population fed on cultivated fruit buds some of the time, or whether some individuals ate them nearly all the time. Unfortunately, fruit trees in 1983 were hardly touched by bullfinches: none of the radio-tagged birds ate apple or pear buds at any time. Bullfinches in this study,

Table 2. Comparison of observations of bullfinch feeding in the present study at Tong, Kent, with those observed by Newton (1964) at Marley Wood, Oxfordshire.

	Ash	All buds	(Hawthorn	Blackthorn	Aspen	Cherry)	Dock	Bramble	Ground
Jan	43	49	15	25	7	2	8	0	0
	(14)	(43)	(35)				(6)	(33)	
Feb	9	86	26	13	46	1	1	1	2
	(16)	(53)	(46)				(2)	(28)	
Mar	5	91	24	50	17	0	0	0	4
	(7)	(79)	(66)				(1)	(14)	

Figures represent time observed feeding on a given plant as a percentage of total feeding time. The figures in brackets are Newton's data averaged over three years, and represent the number of observations expressed as a percentage of total feeding observations.

Table 3. Analyses gut contents of bullfinches trapped on fruit farms. From Newton (1967) and Summers (1981).

	Ash	Wild buds	Fruit buds	Dock	Bramble
<u>January</u>					
Newton	4	0	17	17	23
Summers	55	14	8		
<u>February</u>					
Newton	0	3	68	19	23
Summers	36	54	12		
<u>March</u>					
Newton	1	2	80	39	25
Summers	20	87	13		
average					
Newton	2	2	55	25	24
Summers	40	31	7	23	75

Figures are percentage of birds containing a particular food item. Newton's data are for the winter of 1966 and are based on the gut contents of 288 birds. Summers' data are averaged over 6 winters (1970-1975) and based on 243 birds. Fruit buds included plum and pear buds. Wild buds included hawthorn, blackthorn, and crab apple. The overall average for Summers' data, is for the months November to March for each year.

kept almost exclusively to dense woodland, hedgerows and brambles. It is useful, nevertheless, to compare the feeding records of this study with those made by Newton (1964) and with gut analyses of bullfinches trapped in fruit orchards (Newton, 1967; Summers, 1981).

Table 2 demonstrates some qualitative agreement between observations made on a fruit-farm in Kent and those made by Newton in Marley wood, Oxfordshire. In both cases, bullfinches were seen to eat ash keys less often, and buds more often, as spring approached. Quantitative agreement is less impressive, possibly because of the different way in which the data were measured. At Tong, I was following a particular bird throughout its day. Feeding bouts were therefore timed, and preference for a given food source expressed as the percentage of feeding time devoted to that food. Newton was unable to monitor known individuals and his data concern the percentage of total observations that a bird was seen feeding on a given food source. Since birds must spend longer feeding on buds in order to obtain the calorie equivalent of seeds, then time-based measurements of feeding behaviour may overestimate the importance of buds in the diet. (The Tong study shows birds as concentrating on buds to a greater extent than Newton's study.) However, the same argument applies to Newton's study. If birds are encountered randomly on transect walks, they are more likely to be seen eating buds, since this is a time-consuming activity.

The biggest difference between the studies, is the near absence of bramble seeds in the diet of Tong bullfinches. In Newton's study, one third of all feeding observations in January were of birds feeding on bramble. The simplest explanation for this difference is that the bramble seed was not abundant at Tong farm in January, 1983. Evidence from MacKenzie (1983) supports this suggestion. An average of 24 green fruits per bramble stem was present in August, and less than one dried seed head per stem was left by mid December. Newton's data shows that in different years bramble seeds vary in their availability; they may or may not last the winter. In the winter of 1962-3,, bramble seeds in January, February and March declined to about 80%, 60% and 55%, respectively, of their October numbers. Bullfinches were seen eating them on 46%, 44% and 40% of occasions. In the winter of 1963-64, bramble seeds had declined to 15% of their October numbers by January, and to 10% and 5% by February and March. However, bullfinches feeding on brambles still acounted for 42% and 38% of feeding records in January and February. Only in March did the number of observations of birds on bramble fall to 2%. This suggests that the

consumption of bramble seed by bullfinches is not wholly determined by its abundance. Of course, if there is no bramble seed, then bullfinches will not be recorded eating it. This may explain the results at Tong in 1983, but it is also possible that birds were feeding out of sight, on the ground on fallen bramble seeds.

Newton (1964, 1967) dismisses this possibility -- "Most birch and nettle seeds fall by the end of December, and are then lost to bullfinches which ... do not feed on the ground." In the years of his study, Newton only once observed bullfinches feeding on the ground. Matthews (1983) observed them foraging for fallen ash keys on three occasions, and also concludes that ground feeding is relatively unusual. However, as has already been mentioned, bullfinches are shy birds, preferring dense vegetation to open spaces. In this environment it may be especially difficult to spy them low down. Radio-tracking has the advantage that, even when you cannot for the moment see your subject (which for the bullfinches in this study was 90% of the time), you know where to look for it. You are more likely to discover it in inconspicuous places. Over a two month period, one bird in this study was tracked on ten days, and on five of them was seen to feed on the ground, usually in the company of several other unmarked individuals. Six of the nine tagged birds were also seen to adopt this habit at some time or other. It was usually unclear what they were eating, although fallen ash keys were taken. Bullfinches probably feed on the ground more commonly than has been supposed.

Analyses of gut contents (Table 3) shows that bramble seeds are important in the diet of bullfinches even in late winter when it is less available. Newton (1967) found that nearly a quarter of birds trapped by farmers in January to March contained bramble seed. In a six year study, examining the guts of bullfinches shot between November and March, Summers found bramble seed in three quarters of them. It was the only food which he found in every month of every year.

Although direct sightings of bullfinches eating bramble seeds in the present study were few, it is possible that seed consumption was higher than this would suggest. One area of the study site consisted almost wholly of brambles. Bullfinches were often recorded there, but hardly ever seen. On three days in the second half of January, one bird spent at least five hours a day there. In the same period, another bird spent a total of six hours in these brambles. The natural deduction is that they were

eating bramble seeds, but they could have been resting or feeding on something else.

It may be mistaken to assume that a bird which spends much of its time in a given place is feeding on the most abundant food source there, or that it is feeding at all. For example, Table 4 shows an attempt to correlate bullfinch sightings with abundance of known food plants. The number of radio fixes of bullfinches located in a matrix of 100 x 100 m blocks was recorded separately for the months October to March. Each block contained 200 evenly spaced sampling points at which the presence or absence of a variety of plant species was recorded. (The vegetation survey was carried out by M.A.F.F. and not by me.) Cover indices were calculated for ash, bramble, hawthorn, blackthorn, nettle and three species of dock, *Rumex crispus, R. sanguineus, R. obtusifolius*. In addition, sampling points were categorised as lying in wood, orchard or thicket. The vegetation survey is incomplete at the time of writing, but cover indices have been obtained for 81 of the 100 blocks comprising the study area. A stepwise multiple regression analysis was performed using all blocks. Since there were often many blocks in which bullfinches were never recorded, two further analyses were conducted, a multiple regression analysis including only those blocks in which bullfinches had been recorded and a discriminant analysis in which blocks were categorised as being visited or not visited by bullfinches.

The multiple regression analyses in Table 4 show a strong correlation between presence of bullfinches and abundance of sharp dock *Rumex crispus*. Different variables enter into the discriminant analyses, but *R. crispus* still predominates. Newton (Table 3) frequently found dock in bullfinch guts, and Wright and Summers claim that some sorts are preferred over others (*R. conglomeratus* and *R. sanguineus* in particular) but it is hard to believe that bullfinches were feeding on one particular, not very common, species of dock throughout the winter, and that this is the single most important factor explaining the birds' presence at particular locations. That *R. crispus* appeared to be the most popular food plant in all six months is, again rather unlikely. The analyses fail, for example, to reflect the fact that in some months bullfinches also eat a lot of fruit buds, ash keys and bramble seeds. It would seem that the only sure way of telling what a bird has been feeding upon, is to look at the contents of its gut.

Table 4. Correlations between number of bullfinches and abundance of food plants.

	Multiple Regression				Discriminant Analysis	
	All blocks		Excluding zeros			
	Significant variables		Significant variables		Significant variables	
Oct.	+R. crisp.	R=.64 df=1,79 F=55,7 p<.001	+R. crisp.	R=.66 df=1,10 F=7,6 p<.02 n=12	+Bramble +R. crisp. -Hawthorn +Wood +R. obtus. +R. sang. +Thicket	df=7 χ^2=31,3 p<.001
Nov.	+R. crisp. +Wood -R. sang.	R=.82 df=3,77 F=52,1 p<.001	+R. crisp.	R=.80 df=1,20 F=36,5 p<0,001 n=22	+Wood +R. crisp. +R. obtus. -Blackthorn	df=4 χ^2=45,5 p<.001
Dec.	+R. crisp. +Wood -Ash -R. sang.	R=.75 df=4,76 F=24 p<.001	ns	n=18	+R. crisp. +Wood +R. obtus. -Ash -R. sang.	df=5 χ^2=32 p<.001
Jan.	+R. crisp. +Thicket	R=.79 df=2,78 F=63,7 p<.001	+R. crisp. +R. sang. +Thicket	R=.91 df=3,14 F=21,7 p<.001 n=18	+R. crisp. -Orchard -Ash +Haw +Nettle -Blackthorn	df=6 χ^2=26,4 p<.001
Feb.	+R. crisp. +Hawthorn	R=.59 df=2,78 F=21,2 p<.001	+R. crisp.	R=.57 df=1,24 F=11,8 p<.002 n=26	+Bramble -Ash +R. crisp. +Wood +R. obtus.	df=5 χ^2=21,5 p<.001
Mar.	+R. crisp. +Wood	R=.36 df=2,78 F=5,7 p<.005	ns	n=19	+Wood -Bramble +R. crisp. +R. obtus.	df=5 χ^2=43,3 p<.001

Plus and minus signs refer, in the case of multiple regressions, to the direction of correlation between abundance of food source and number of bullfinch records, controlling for variables already entered into the analysis. In the case of discriminant analyses, signs refer to the direction of correlation between the food plant abundance and the standardised discriminant function.

1.d. Wild buds and cultivated buds

Newton (1967) and Summers (1981) both obtained their birds in or around fruit orchards, yet the proportion of them found to have been eating cultivated fruit buds was very different (Table 3). Newton's birds preferred pear buds to wild buds, while bullfinches in Summers' study took mostly hawthorn and blackthorn buds. Newton writes that "buds of fruit-trees are preferred to hawthorn and other native species. Although the latter were available in plenty, they were not taken before the end of February, and then only in small quantity compared with fruit buds." The reason he puts forward for this preference is that wild buds were smaller than cultivated buds. Summers also notes that in 1969-70 when spring was late and wild buds were small (0.5 mg compared with the usual average of 0.8 mg) then fewer of them were eaten. Even so, more birds contained wild buds than fruit buds in March of that year.

At Tong farm, birds were never seen eating cultivated buds, although, since this was a fruit farm, there was no shortage of them. Despite their smaller size, they were often seen eating hawthorn and blackthorn buds (55% of total feeding observations). (A single clump of aspen trees, which have much larger buds, accounted for 30% of observed feeding time.) Matthews and Flegg (1981) argue that bullfinches can compensate for the smaller size of hawthorn and blackthorn buds by eating them more quickly. My own observations support this.

Eight radio-tagged birds were seen feeding on buds. Blackthorn buds were conspicuously smaller than the hawthorn buds on which bullfinches chose to feed (see also Matthews, 1983). Hawthorn buds were in turn, much smaller than aspen buds. Blackthorn buds seemed to be plucked and swallowed immediately, whereas the larger hawthorn buds were often "husked" before swallowing, in the manner described by Newton (1964) for fruit-buds. According to Matthews (1983), whole blackthorn buds are as digestible as the flower initials of pear buds, and more digestible than whole hawthorn buds. Clusters of aspen buds were not plucked, but left on the branch and bites taken out of the side. Information was collected on feeding rates by counting pecks into a portable cassette recorder, and timing, to the nearest tenth of a second, the intervals between pecks. Figure 1a shows peck rates for hawthorn, blackthorn and aspen buds, separately for each of the birds.

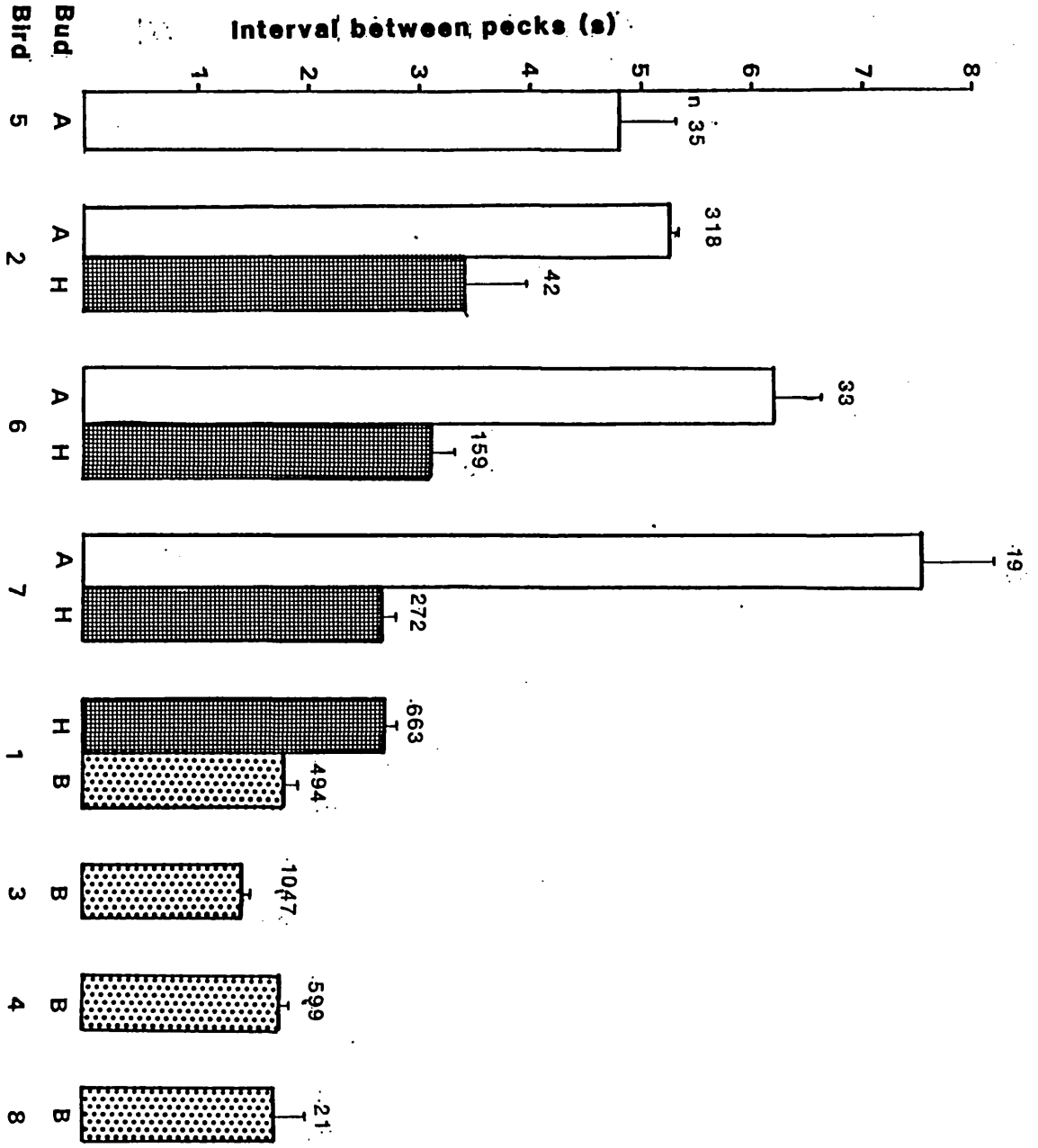


Fig. 1a

Intervals between pecks for Aspen, Hawthorn and Balckthorn buds, shown separately for each bird.

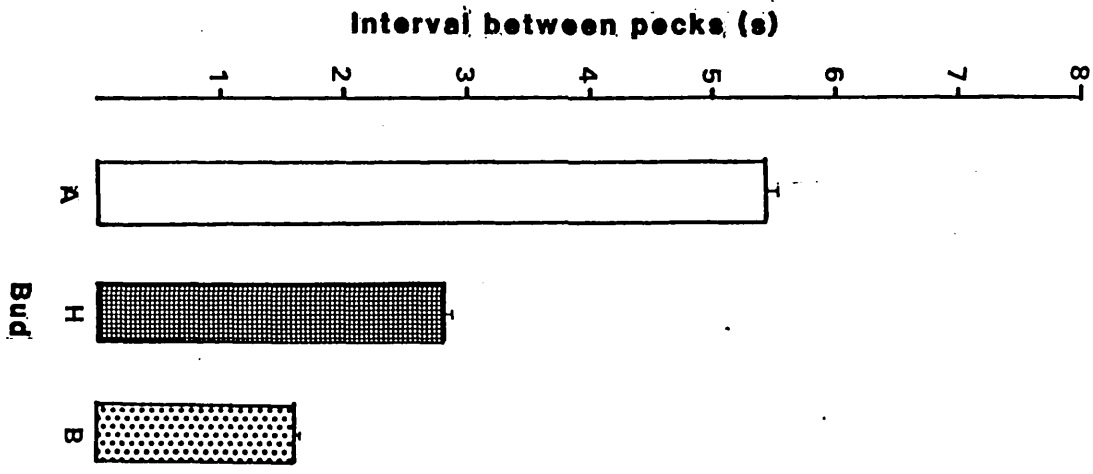


Fig. 1b

Intervals between pecks for Aspen, Hawthorn and Blackthorn buds. Combined data.

Only bird 1 was seen to feed on blackthorn and on hawthorn. For this bird, records of hawthorn feeding all occurred in February, while those for blackthorn were all made in March, when buds might be expected to be larger. Nevertheless, blackthorn buds were eaten significantly faster (see Table 5). Three birds (2, 6 and 7) were seen to feed both on hawthorn and aspen. In each case, pecking rates on aspen were significantly slower than those for hawthorn. Data for combined birds (Fig. 1b) shows that the rate of feeding was faster on blackthorn than on hawthorn than on aspen buds. Matthews (1983) notes that on his study site, birds were rarely seen feeding on hawthorn, although it was abundant. At other sites, where blackthorn was common, he often saw bullfinches taking buds. A vegetation survey of the Tong study site showed blackthorn to be much less common than hawthorn. Blackthorn was found at only 22 sampling points (out of a total of 16,200 points spaced 5 m apart over the study site); the figure for hawthorn was 405. Yet blackthorn appeared to be the more popular source of buds, accounting for 30% of feeding time, compared with 24% for hawthorn.

Table 5. T-test comparisons of Pecking Rates on Aspen, Hawthorn and Blackthorn.

Bird	bud	Peck intervals (sec)	se	n	t	p
1	blackthorn	1.8	0.11	494	5.9	<0.001
	hawthorn	2.7	0.10	663		
2	hawthorn	3.4	0.52	42	3.6	<0.001
	aspen	5.3	0.17	318		
6	hawthorn	3.1	0.21	159	6.1	<0.001
	aspen	6.2	0.45	33		
7	hawthorn	2.7	0.13	272	9.4	<0.001
	aspen	7.5	0.66	19		

2. BULLFINCH RANGES

2.a. Method

Between September 1982 and December 1984, *Biotrack SS1* radio-transmitters were attached to 63 birds caught in mist nets at the Tong farm study site. As part of a long term study (Greig-Smith, 1985), I personally tracked about 20 of them. Some birds were captured and recaptured several times, so that a total of 80 transmitters were used. They weighed either 2.0 or 2.5 g and worked for between 3 and 8 weeks depending on the size of battery used. The battery and transmitter were sealed in epoxy resin and a guitar string was used for an aerial. The package was glued to a brightly coloured plastic strip and with the aid of nylon string, was worn by the bird on its back like a rucksack (plate 2). Bullfinches weigh about 20 g and, given a few minutes to adjust, they seemed able to cope with the extra load. Very few birds failed to fly off when released. Birds caught towards dusk, were kept and fed overnight and let go the following morning.

Birds were followed on foot using a hand-held receiving aerial. Under average conditions signals could be traced up to 750 m away. When birds were feeding on the far side of an obstruction, they were less easy to find. Once found, a bird's position was mapped on a grid of 25x25 m squares as a single record. An interval of at least half an hour was allowed to pass before another record could be made for the same bird. No bird provided more than 20 records in a single day. If a bird could not be found near its usual place and no signal could be heard elsewhere within the study site, the observer would search for it around the site perimeter. If a bird was still not located, an attempt was made to find it, later, by driving to local high points, where the chances of picking up signals was greater.

There are many different ways of plotting a home range (see Voigt and Tinline, 1980; Trevor-Deutsch and Hackett, 1980; and MacDonald et al., 1980). Home ranges in this study were established according to the method described by Dixon and Chapman (1980). The distance of every grid intersection point from every bird record was measured and the harmonic mean calculated (Fig. 2a). This gives a matrix of (harmonic) averages for

Plate 2.



Female bullfinch carrying a radiotransmitter.

Fig. 2

Harmonic mean method of calculating home ranges

a) The distance is calculated of each of the intersection points J_1 to J_{36} from each of the sightings X_1 to X_4. The harmonic average of these distances is calculated for each intersection points.
Thus, for the intersection point J_{19}, the harmonic average of the distances from each of the four sightings is given by

$$\frac{1}{\frac{1}{4} \cdot \left(\frac{1}{R_{19,1}} + \frac{1}{R_{19,2}} + \frac{1}{R_{19,3}} + \frac{1}{R_{19,4}} \right)}$$

b) Each of the intersection points J_i now has a numerical value representing a harmonic average. The lower this number, the closer the intersection point is to a centre of activity. Drawing lines which join intersection points of the same value results in a series of contours around activity centres. A value is found which encloses 95% of all the sightings and this delineates the home range.

In the hypothetical example shown, h_1 is the lowest harmonic mean and represents the centre of the bird's range: h_2 represents a local activity centre some distance away.

The dotted line encloses the home range as calculated by the Minimum Area Method, wherebye the smallest convex polygon is drawn around 95% of the sightings. The range established by this method includes large areas where the animal has never been sighted. Similarly, the centre of the range as given by the arithmetic mean (a) is remote from the areas where the animal is commonly seen.

Fig. 2a

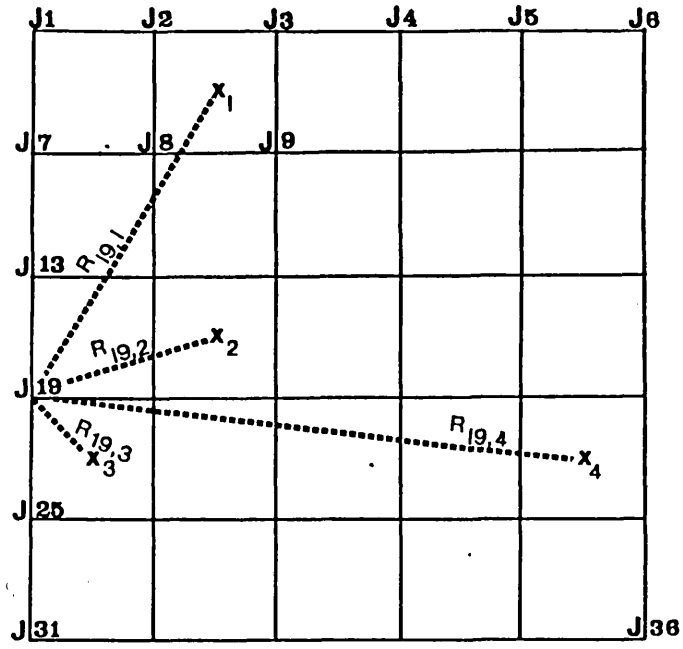
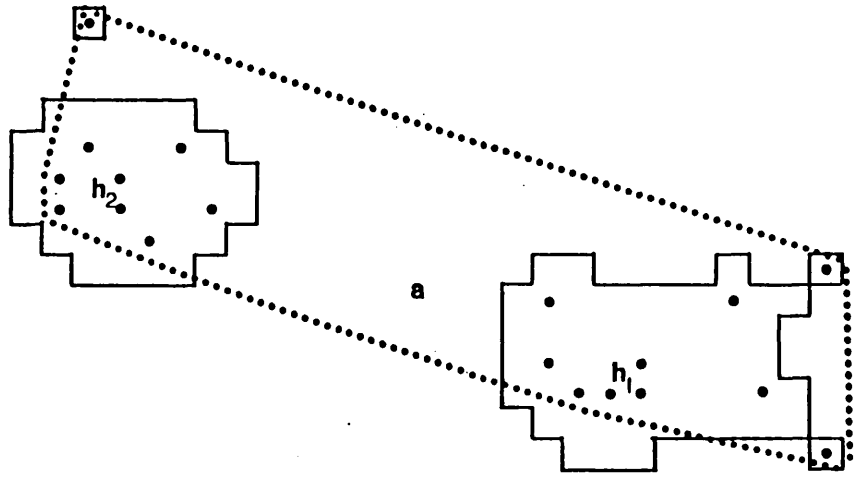

J1
J2
J3
J4
J5
J6
J7
J8
J9
J13
J19
J25
J31
J36
x_1
x_2
x_3
x_4
$R_{19,1}$
$R_{19,2}$
$R_{19,3}$
$R_{19,4}$

Fig. 2b


h_2
a
h_1

each of the intersection points. The lower the figure, the nearer it is to a centre of bird activity. By drawing lines which join intersection pointsof equal value, a series of isopleths or contours emerge which encircle the activity centres. The home range is deemed to be delineated by the isopleth which encloses 95% of bird records (Fig. 2b). The advantage of this method is that it is sensitive to the fact that animals may, simultaneously or sequentially, have more than one centre of activity (see for example the home range for bird 21, and Fig. 2b). When animals have several separate areas of activity, then the centre of the range as calculated by harmonic mean method is bound to lie in one of these areas. When the arithmetic mean (based on orthogonal axes) is used, the centre may fall between two areas of activity at a point where animals are rarely or never found. Similarly, when there are several activity centres, the area of a home range established by harmonic means, will be smaller and biologically more meaningful than that arrived at by other methods. For example, a common way of establishing a home range (the Minimum Area Method) has been simply to draw a single convex polygon which encloses 95% of the records. In the case of of the imaginary bird in Figure 2b this would exclude the outlying extreme of the animal's range but would include large central areas where the bird was never recorded. The harmonic mean method, by allowing centres to be enclosed separately, gives a more parsimonious fit.

Dixon and Chapman found that seven records were enough to establish a home range. In this study birds were often intensively monitored for short periods (up to 20 records in a day), and then ignored for several days. If birds were slowly expanding or shifting their ranges, then an analysis based on many records taken over only one or two days would fail to detect it. It was therefore decided to include only those birds which had been monitored on at least 7 different days. By this criterion 23 birds qualified for home range analysis. Bird 10 qualified twice in successive winters. (Home range plots for each bird may be found in Appendix 1, where a map of the study area showing the main kinds of vegetation is also included.)

The space within a given home range, may not be evenly used. Animals may be found more often in some areas than others. Samuel et al. (1985) describe a test for determining the size of these core areas. The 25x25 m squares within a home range, were ranked in order of intensity of use (i.e. number of bird records) and Kolmogorov-Smirnov test performed against

Table 6. Size of home range, core area and background information on 23 radio-tagged birds.

Bird	Sex	Age	Home Range (ha)	Core Area (ha)	No. + cells*	No. Records	No. Days Tracked	Capture Date	Time Span (days)
1	f	y	1,69	0,5	16	73	11	28-09-82	24
2	m	y	1,06	0,37	14	51	8	06-10-82	15
3	m	o	20,94	1,94	51	424	43	04-01-83	69
			(5,81	0,81	17	132	16		26)
			(16,75	1,5	24	88	9		11)
4	f	y	4,19	0,69	23	417	46	06-01-83	67
5	m	y	12,37	1,6	25	72	13	06-01-83	20
6	m	y	1,31	0,3	14	114	13	10-01-83	17
7	m	o	3,62	0,6	19	165	26	21-02-83	46
8	f	o	1,31	0,25	9	98	13	22-02-83	25
9	f	y	5,37	0,69	14	140	15	01-03-83	23
10	f	y	1,31	0,3	9	115	12	03-03-83	20
11	m	o	5,56	0,94	15	37	9	30-06-83	14
12	f	o	4,62	1,19	19	60	12	30-06-83	17
13	f	o	6,19	0,94	15	77	18	07-10-83	53
14	f	y	5,12	0,94	15	48	14	14-10-83	42
15	f	o	10,19	1,62	26	72	19	04-11-83	110
10	f	o	2,62	0,56	15	105	24	24-11-83	93
16	m	o	0,75	0,31	9	23	9	16-02-84	26
17	f	o	4,37	1,00	25	193	28	02-08-84	35
18	m	o	7,25	1,50	35	251	33	05-08-84	40
19	j	y	5,06	1,19	22	112	15	26-08-84	19
20	f	y	2,56	0,50	8	72	10	13-11-84	24
21	m	y	2,19	0,62	15	106	14	13-11-84	37
22	f	y	4,75	1,00	19	106	14	13-11-84	37
23	f	o	4,31	0,94	15	72	10	28-11-84	25
average =			4,32	0,81	17	113	17		37

* No of + cells = Number of different 25x25m squares in which a bird was recorded, m = male, f = female, j = juvenile; y = younger, first-year birds, o = older, adult birds. Males and adults had larger ranges than females and young birds but the differences were not significant. The number of days tracked refers to the number of different days on which a bird was recorded; the duration means the number of days between capture date and the last record. The core area of bird 3 was destroyed midway through monitoring. The figures in brackets represent its home range before disturbance (before 30 January) and its new home range after moving to a new site (after 26 February). Some birds were recaptured during monitoring and new transmitters attached. Two home ranges have been plotted for bird 10, because it was recaptured in two successive winters.

the null hypothesis that this distribution was uniform (i.e. all squares are used equally). The point at which the ordered cumulative distribution function becomes significantly different from uniform, gives the cut off point for those squares which are used significantly more frequently than average. These squares constitute the core area.

2.b. Results

Some birds (e.g. 3, 4) recieved special attention, being continuously monitored from dawn till dusk; they amassed a disproportionately large number of records (Table 6). We need to check that this did not distort the analysis of home ranges. Table 7 shows that as the number of records for a bird increased, so did the number of different locations in which it was found. But this did not affect the size of its home range or its core area. (A similar result was obtained using the number of days on which a bird was tracked.) Therefore, the unequal effort spent tracking some birds seemed to have little influence on home range area, as determined by the harmonic mean method. (Voigt and Tinline (1980) report that with many measures of home range, area usually increases with sample size.) Core area, home range size and the number of different cells in which a bird was found were each positively correlated with the time span over which a bird was monitored, but none significantly so.

Table 7. Pearson correlations between measures of range size, and frequency and duration of monitoring.

	Home range	Core Area	+ cells
No. of records	.065	.070	.50*
No. of days tracked	.202	.228	.617**
Time span	.224	.214	.225

* $p < .02$, ** $p < .002$, 2-tailed.

Of the sixty three birds which were trapped and supplied with radio-transmitters forty two were first-year birds, and 21 were adults. First-years were retrapped on 10 occasions, while the adults were retrapped 7 times. In other words, proportionately more adults than first-years were caught again at a later date. The difference is not significant but Greig-

Smith (1985a) provides evidence from a much larger sample that the proportion of first-year bullfinches caught in mist nets declines from around 75% of the population in September to 50% by the following breeding season. This suggests either that first-years were more adept at avoiding mist nets, or that they were dispersing over a larger area or were dying at a faster rate than were adults. The first alternative is the least likely; we would expect first-years to be less skilled at avoiding capture.

There is some direct evidence on mortality. Of the 63 radio-tagged birds, 16 died while their radios were still transmitting, and their remains were located. Most of them had been eaten by predators -- blood and feathers were found by the transmitters. Eleven of the birds were first years and five were older birds. Since first-years already outnumbered older birds by two to one in the parent sample, then this suggests that the death rate was similar for both age-groups. However, none of these birds survived for very long. On average, they were found dead within 7.4 days of being radio-tagged and released. Older birds that died tended to survive longer (10 days) than first years (6.3 days). It is likely that these deaths were hastened by the extra burden of carrying the radio-transmitter, and that they do not reflect the natural mortality statistics. It looks as if birds which survive the first week wearing a radio-harness, are likely to outlive the battery.

There is indirect evidence that first year birds "disappeared" sooner than adults. Twenty-four home ranges were plotted for birds which had been monitored on at least seven days (Table 6). Half of them were for adult birds, so that young birds, more numerous in the general population, were under-represented in the sample. Furthermore, we were able to track adults over longer periods of time, for 46 days on average, as opposed to 29 days for first year birds ($t=1.77$, $df=22$, $p=.09$). Transmitter or battery failures should have occurred no sooner among first years than adults. The first-years which disappeared early may have been leaving the study area. (It is also possible they were killed and their transmitters damaged or carried off out of range e.g. out of the study area, or below ground.)

Evidence from ringing and recapture studies suggests that bullfinches rarely migrate more than 5 km away from the place where they were originally caught, and that most birds stay within 2 km of the ringing site (Summers, 1979; Greig-Smith and Wilson, 1984). In the present study only one bird was tracked to a point more than 1 km distant from the its capture point. Two birds appeared to have home ranges whose centres lay

outside, but within 200 m, of the study site perimeter. All other birds which disappeared sooner than expected, did so suddenly -- there was no gradual drift of position -- and were never heard of again, despite attempts to find them within a 2 km radius of the study centre. This suggests that if young birds were indeed dispersing, they were doing so in discrete jumps of at least 1 or 2 km.

As yet, the data are too sparse to distinguish between transmitter failure, dispersal and death. The home ranges plotted for the birds in Table 6 and appendix 1 may not be representative for all birds at all periods in their lives. However, they show that many bullfinches remain faithful to very local areas (of about 4.5 ha) for several weeks at a time. In the winter of 1983/4, bird 10 occupied a home range of 1.3 ha, more than 80% of which was encompassed by its expanded range (2.6 ha) the following year. The centre of activity scarcely shifted between seasons.

Figure 3 shows a series of isopleths constructed from the combined records of all birds. The points A, B and C are the three most commonly used netting sites, and it can be seen that they coincide with the three areas of greatest activity. Examination of the plots for individual birds (appendix 1) shows that only in two cases did a home range encompass more than one netting site, even though they were less than half a kilometre apart. There was a great deal of overlap, however, between birds netted at the same site.

Table 8a shows that the home ranges of two birds from site A (7 and 8) did not overlap any of six birds caught at site B and tracked during the same winter (1982/3). Among the site B birds, however, there was an average overlap between any two birds of 64%. The two site A birds shared, on average, 67% of their respective home ranges. Other authors (eg Ewer, 1968, quoted in Dixon and Chapman, 1985) note that whereas animals may share large parts of their home ranges, overlaps between core areas are less common. The data for bullfinches however, suggests that birds with overlapping home ranges, also share their core areas. There was a 54% and 70% core area overlap for the six site B birds and the two site A birds, respectively. In general, the bigger the overlap between home ranges, the bigger the overlap between core areas ($r=0.82$, $n=30$).

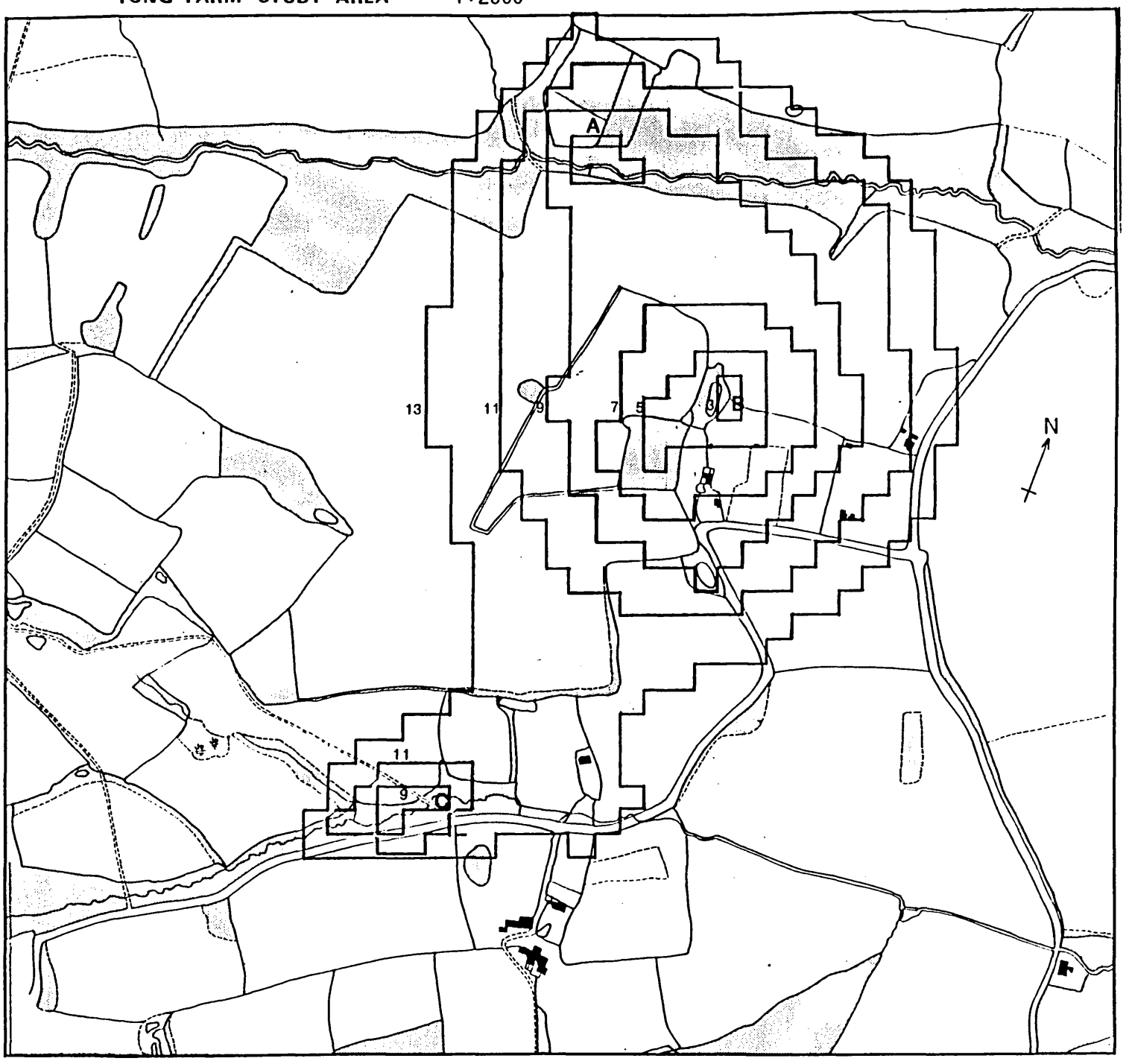


Fig. 3

Contours of bullfinch activity in relation to the three most commonly used netting sites (A, B, C). The lower the number, the greater the activity.

Table 8a Percentage overlap of home ranges and core areas plotted for eight birds tracked during winter 1982/3

	3^B	4^B	5^B	6^B	7^A	8^A	9^B	10^B
3^B	*	59	91	21	0	0	69	23
	*	*54*	*69*	*23*	*0*	*0*	*31*	*15*
4^B	82	*	100	28	0	0	94	31
	64	*	*82*	*36*	*0*	*0*	*64*	*45*
5^B	43	34	*	11	0	0	43	11
	36	*36*	*	*20*	*0*	*0*	*36*	*20*
6^B	95	90	100	*	0	0	90	52
	60	*80*	*100*	*	*0*	*0*	*100*	*0*
7^A	0	0	0	0	*	34	0	0
	0	*0*	*0*	*0*	*	*40*	*0*	*0*
8^A	0	0	0	0	100	*	0	0
	0	*0*	*0*	*0*	*100*	*	*0*	*0*
9^B	74	73	99	22	0	0	*	24
	36	*64*	*100*	*45*	*0*	*0*	*	*36*
10^B	100	100	100	52	0	0	100	*
	40	*100*	*100*	*0*	*0*	*0*	*80*	*

For a pair of birds (S_1 and S_2) whose home ranges (A_1 and A_2) overlap by an area A, the percentage of S_1's home range that is shared with S_2 is given by $(A/A_1) \times 100$, and the percentage of S_2's home range shared by S_1 is given by $(A/A_2) \times 100$. The two values are rarely the same. Thus the range of bird 8 is entirely encompassed by that of bird 7, but the latter, having a larger territory, only shares 34% of its range with 8. The superscripts A and B refer to the netting sites at which the birds were trapped. The figures in italics are for core areas.

Tables 8b-d confirm the finding that the overlap between home ranges of birds netted at different sites is small, the largest being one of 27% between birds 20 and 23 in the winter of 1984/5. Looking at the individual plots (appendix 1) it may be seen that all three birds netted at site B (20, 21, 22) had home ranges with two separate centres of activity, and yet the overlap between them was still quite high (48% for home ranges, 37% for core areas). These birds and bird 23 shared only 11% of their home ranges despite the fact that they all frequented the same piece of woodland surrounding site A. The home ranges of birds 21 and 22 in particular seemed to be fitted around, but not to overlap, that of bird 23.

This raises the possibility that bullfinches associate in groups which avoid other groups.

The history of bird 3 is interesting in this respect because its home base near site B was cleared for grass seeding, and the bird was obliged to move elsewhere. Shortly after the destruction of its usual site, while it was feeding in a hawthorn tree north of site A, I saw it chased nine times in succession by another male bird; the longest run of sustained aggression witnessed during the study. Nevertheless within a week or two, bird 3 appeared to have successfully established itself at site A.

As well as having similarly shaped home ranges, birds 21 and 22 travelled as a pair for some of the time. Figure 4 shows their movements between netting site B and their other centre of activity to the east of site A. Between 13th and 21st of November their paths coincided exactly, but became uncoupled later on. Of 101 occasions when the locations of both birds were mapped at the same time, bird 22 moved between sites 25 times and bird 21, 21 times. Both birds moved together and in the same direction seven times. The probability (P) of this happening by chance is given by

$$\sum_{p}\sum_{q}^{a\ b} \frac{\frac{n_1!}{p!.(n_1-p)!} \cdot \frac{n_2!}{q!(n_2-q)!} \cdot \frac{n_3!}{(a-p)!.(b-q)!.(n_3-(a-p+b-q))!}}{\frac{n_4!}{a!.b!.(n_4-(a+b))!}}$$

Where n_1 = No. of moves from B to A by bird 22; n_2 = No. of moves from A to B by bird 22; n_3 = No. of times bird 22 did not move; n_4 = total No. of records; p = No. of times both birds simultaneously moved from B to A; q = No. of times both birds simultaneously moved from A to B; a = No. of moves from B to A by bird 21; b = No. of moves from A to B by bird 21. Substituting in the actual values (n_1=13, n_2=12, n_3=76, n_4=101, p=3, q=4, a=10, b=11) gives,

P = 0.00065

Therefore, birds 21 and 22 were more likely to move together than would be expected by chance. This strengthens an impression I had, while monitoring birds in the field, that they often arrived and/or left an area in pairs or small groups, (though see Greig-Smith, 1985a, in which it seems that bullfinches move independently between ash trees). Wilkinson (1982) observed bullfinches over two winters and saw them most often in groups

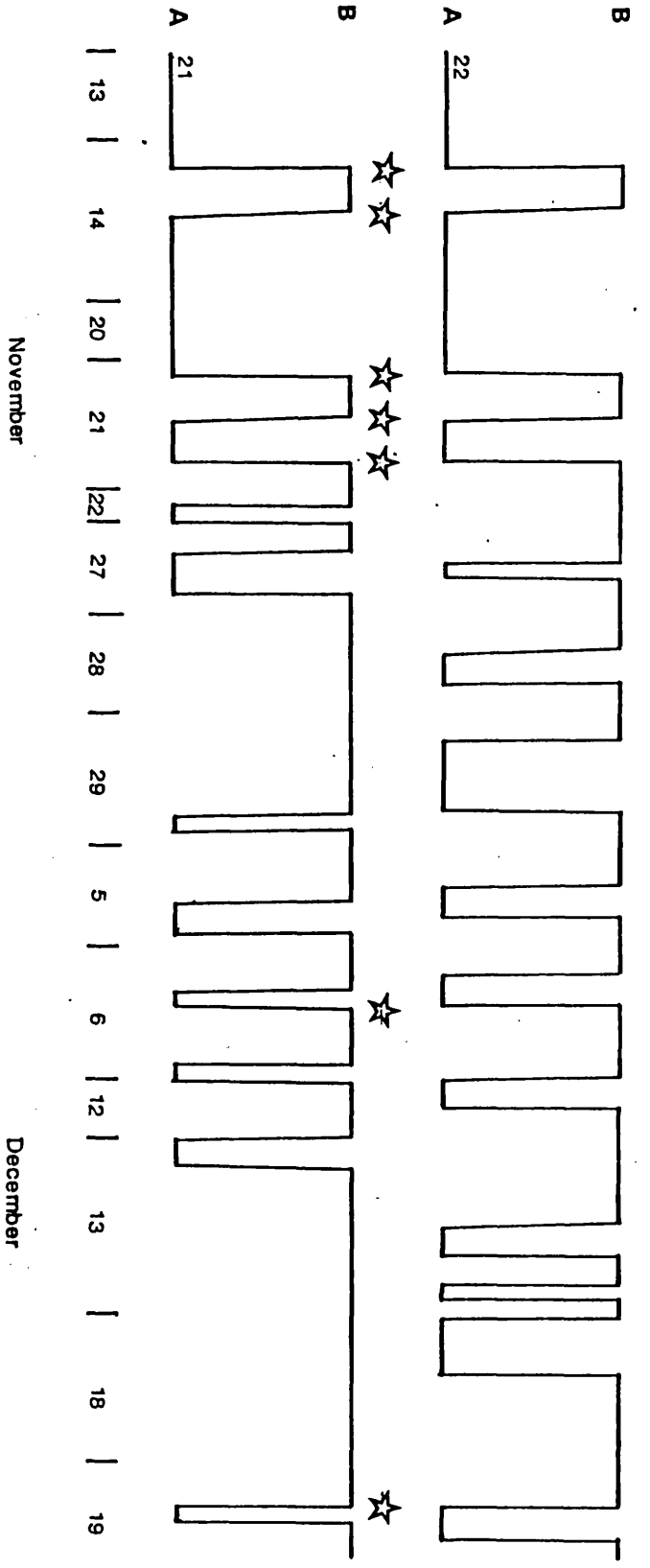


Fig. 4
Movements of birds 21 and 22 between two sites (A and B)
Stars indicate when both birds moved between sites at the same time and in the same direction.

of one. However, 30% of his sightings were of bullfinch pairs. His population was not ringed and therefore he had no data on associations between known individuals. Associations between bullfinches are difficult to prove, because although individuals may be found together at a given place, they don't move about much, at least not far enough or often enough to be sure that they are acting together rather than merely aggregating at favoured feeding places. Birds 21 and 22 were an exception because they regularly commuted between clearly separate feeding sites. It remains a possibility that there was no genuine social attraction between these individuals and that they were merely responding to a series of disturbances or contingencies in the same way. A genuine association in this case would contradict Greig-Smith and Wilson's (1984) finding that bullfinches range between sites independently of each other. They found that pairs of birds which ranged between two netting sites were less likely to be trapped together than birds which kept to a single site. They also concluded that birds spend most of their time close to one site with occasional excursions to the other. Possibly, the lack of association between ranging pairs was because members of a given pair were more likely to inhabit different "home" bases. A fairer comparison would look at the association between ranging birds known to spend most of their time at the same site. In other words, given that bullfinches tend to keep within a definite locale, with rare excursions out of it, then birds sharing the same locale are likely to be trapped together, whether or not they genuinely associate with each other. Birds which range between sites are more likely to be caught among "strangers".

Table 8b. Percentage overlap of home ranges and core areas plotted for five birds tracked during winter 1983/4.

	13^{B}	14^{B}	15^{D}	10^{B}	16^{D}
13^{B}	*	14	0	24	0
	#	*7*	*0*	*27*	*0*
14^{B}	17	*	0	0	0
	7	#	*0*	*0*	*0*
15^{D}	0	0	*	0	1
	0	*0*	#	*0*	*4*
10^{B}	57	0	0	*	0
	44	*0*	*0*	#	*0*
16^{D}	0	0	75	0	*
	0	*0*	*20*	*0*	#

Table 8c. Percentage overlap of home ranges and core areas plotted for four birds tracked during winter 1984/5.

	20^{B}	22^{B}	21^{B}	23^{A}
20^{B}	*	44	39	27
	#	*37*	*37*	*25*
22^{B}	24	*	43	10
	19	#	*37*	*19*
21^{B}	46	94	*	1
	30	*60*	#	*10*
23^{A}	16	11	1	*
	13	*20*	*7*	#

Table 8d. Percentage overlap of home ranges and core areas plotted for two birds tracked during autumn 1982, summer 1983 and for three birds during summer 1984.

	autumn 1982	
	2^B	1^B
2^B	*	76
	#	*83*
1^B	48	*
	62	#

	summer 1983	
	12^C	11^C
12^C	*	99
	#	*87*
11^C	82	*
	68	#

	summer 1984		
	17^C	18^C	19^C
17^C	*	32	49
	#	*50*	*50*
18^C	22	*	35
	33	#	*25*
19^C	57	59	*
	42	*32*	#

3. DISCUSSION AND CONCLUSION

The data obtained from radio-tracking individual birds largely agree with those obtained from mark-recapture studies. In the years of this study, bullfinches spent most of their time within home ranges occupying less than 5 ha. Some birds would commute between several separated activity centres, but these centres were never more than 500 m apart. Excursions outside the normal home range were also rarely more than 500 m distant. If the data from these birds and for these years are typical, then the culprits taking most buds in a given orchard will probably be resident bullfinches. The same conclusion has been drawn by Greig-Smith and Wilson (1984) using mist netting data from the same study site in 1981 and 1982. They found that certain individuals were caught repeatedly at the same site over a 15 month period. Eighty four percent of birds recaptured at a given site had previously been caught at the same site. Nevertheless a quarter of all birds recaptured were eventually caught at both netting sites, indicating that excursions of 350 m (the distance between sites A and B) were not uncommon. Matthews and Flegg (1981) have also conducted studies of bullfinch movements at a site very near to Tong farm, and they come to different conclusions.

> In winter there are probably hundreds of bullfinches within reach of any orchard wherever suitable habitat occurs. Ringing studies indicate that they are mobile and probably visit several different orchards over a period of time, although movement for distances greater 5 km is unusual. The damage in orchards, therefore, is often done by many birds and not by 'just a few locals'.

Matthews and Flegg are probably correct in arguing that birds may visit several orchards given time. However, the radio-tracking data clearly show that they remain faithful to small areas for several weeks at a time, with relatively few excursions further than a few hundred metres. The majority of birds present in a given orchard at a given time will have fed there before and will feed there again. This has implications for the use of repellents. It means, for example, that repellents which rely on conditioned aversion would be more likely to succeed in deterring bullfinches. Conditioned aversion requires an animal to learn that a food with a particular taste or colour will make it feel ill later on. If birds are highly mobile, sampling many foods from many places in a short time,

then they might not be able to learn this association. Similarly, if tannin based chemicals were used as repellents, it may need repeated experiences for birds to associate a particular flavour with the tannins' effects on digestive efficiency. The evidence from Greig-Smith et al. (1983 and in preparation) that bullfinches are sensitive to secondary plant compounds, in the absence of any other cues, is encouraging.

Repellents are likely to be most effective where an animal can find other sources of food apart from the treated crop. If it must feed on this crop or else die of starvation then repellents will probably be useless. In the case of bullfinches, there are likely to be several alternatives to cultivated fruit buds. If the main problem is bud losses along the outer rows, then repellents applied to these trees may encourage birds to move further into the orchard and spread their damage. Hedgerows and woodland thickets usually offer an abundant supply of hawthorn and blackthorn buds, which may be preferred to treated cultivated buds. Although Newton (1967) argued that bullfinches always prefer cultivated to wild buds (because the former are bigger and more material can be eaten in a given time), my own data contradict this. Birds in my study were seen to feed for prolonged periods on wild buds, while abundant supplies of pear and apple buds close by remained untouched. Furthermore, birds appeared to compensate for the small size of wild buds by eating them more quickly. It would seem that the preference for wild buds or cultivated buds is relatively fickle, or at least that the difference in their attractiveness is not extreme. A small reduction in the palatability of fruit buds, through the application of repellent, may be enough to encourage bullfinches to feed on something else.

APPENDIX: Maps of study site and individual home ranges

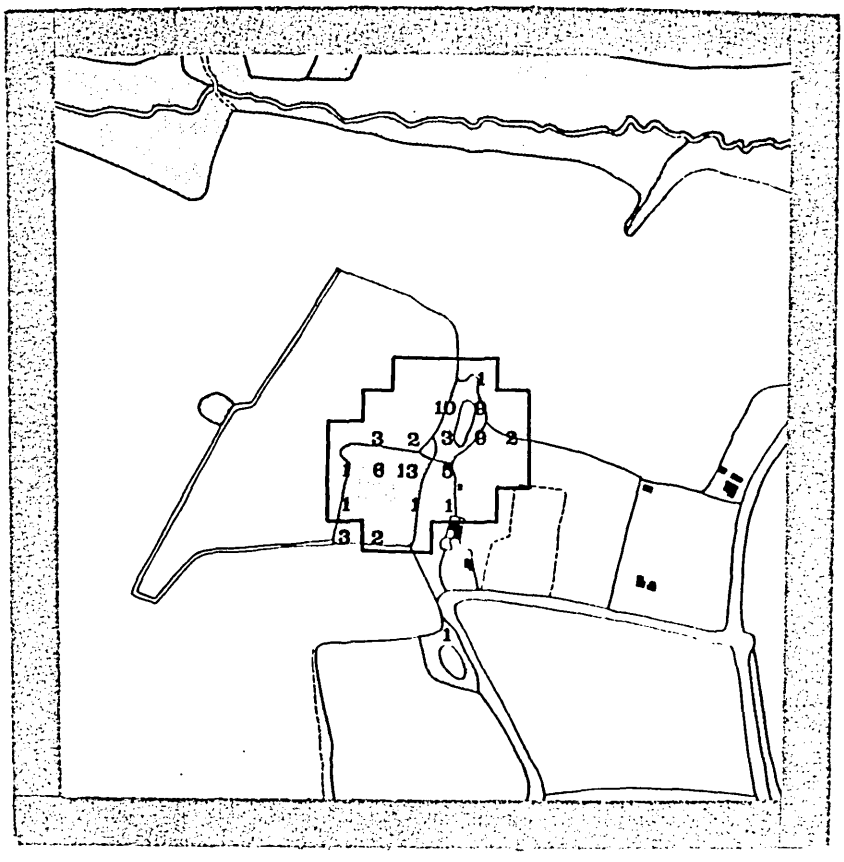
TONG FARM STUDY-AREA 1:2500



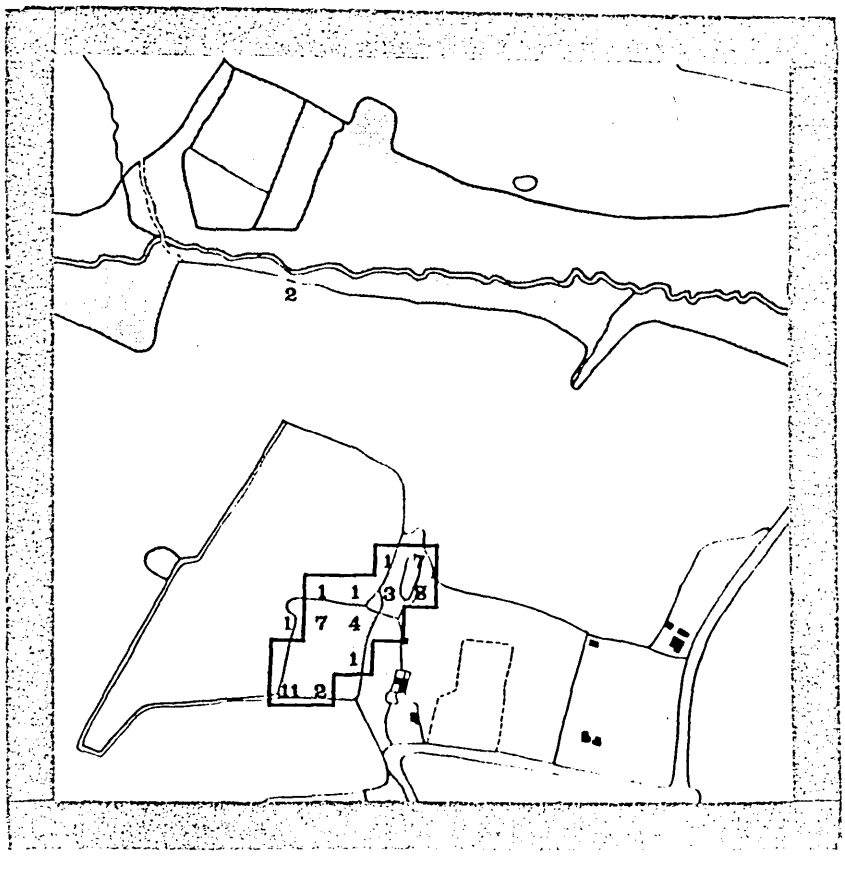
The study site. A, B, C are the main netting sites. Shaded areas represent woodland. Circles show the location of ash trees.

Home ranges of the birds listed in Table 6. The numerals represent the number of sightings of a bird at that location.

Bird 1

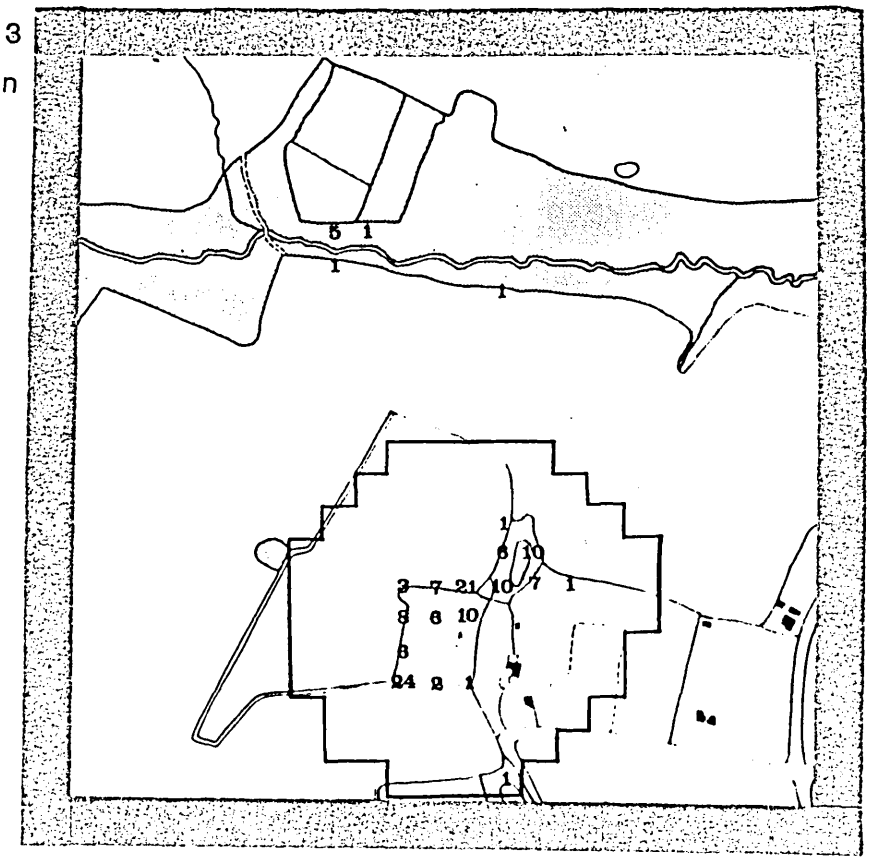


Bird 2

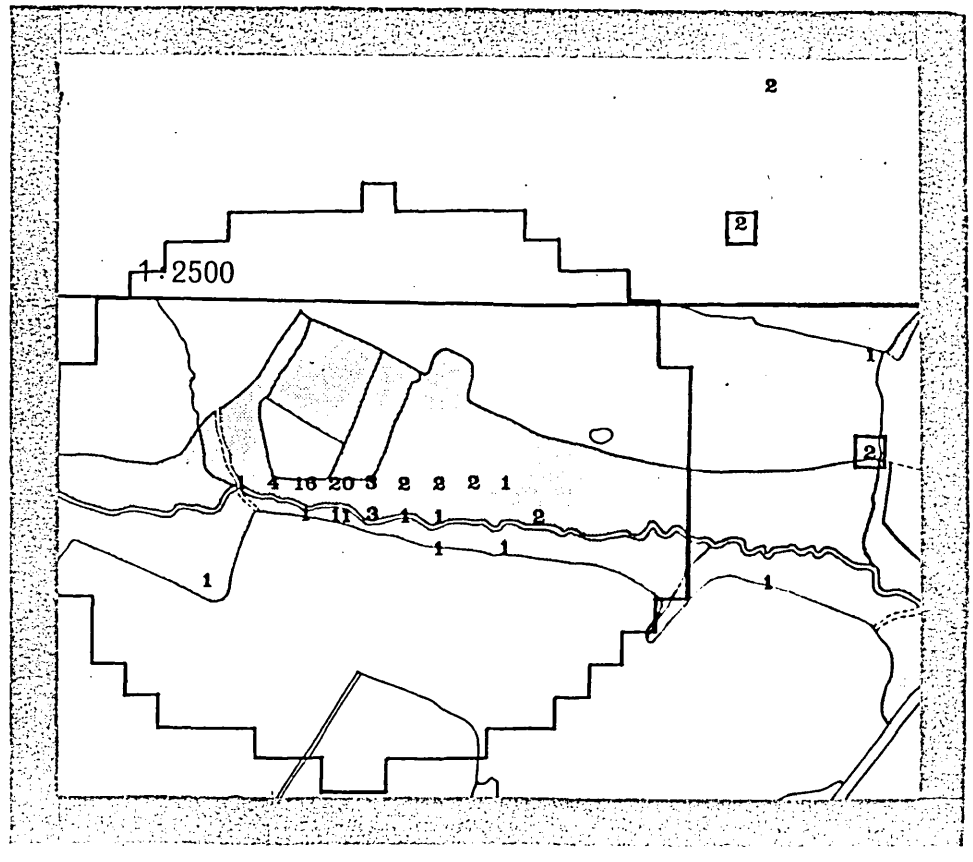


Bird 3

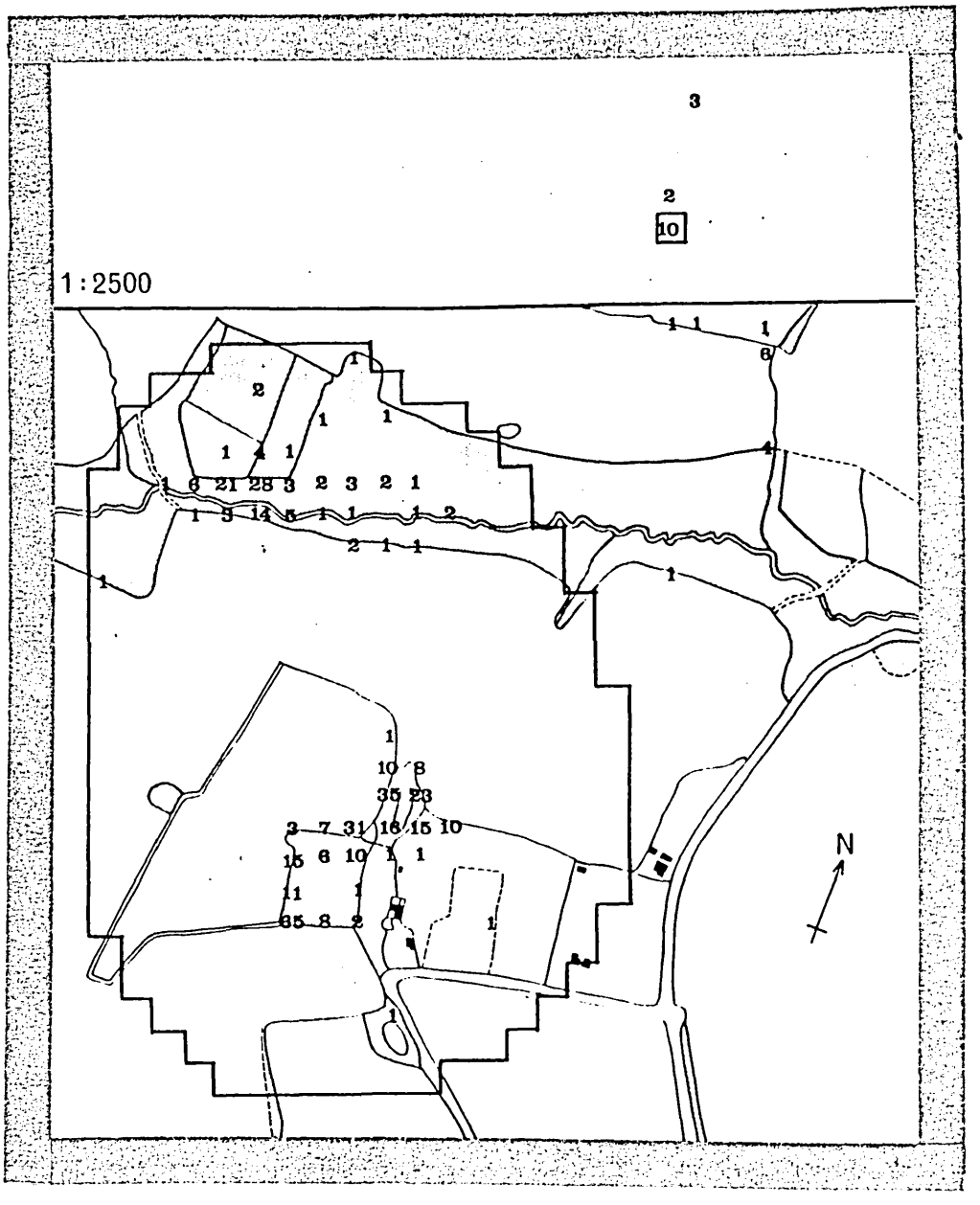
4-29 Jan



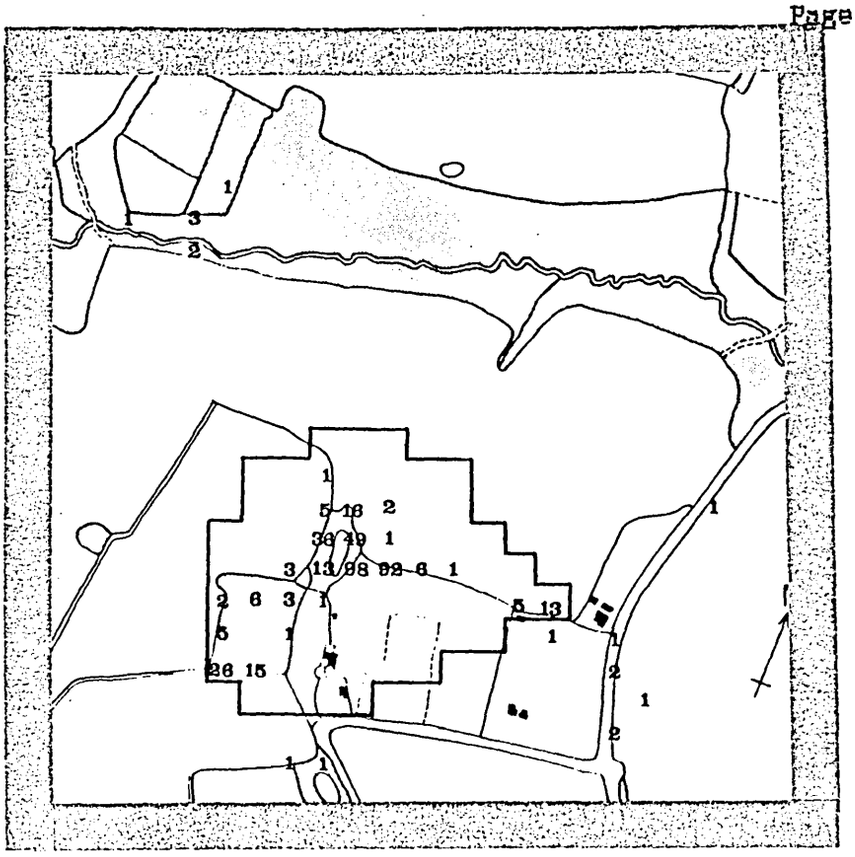
26 Feb - 13 Mar



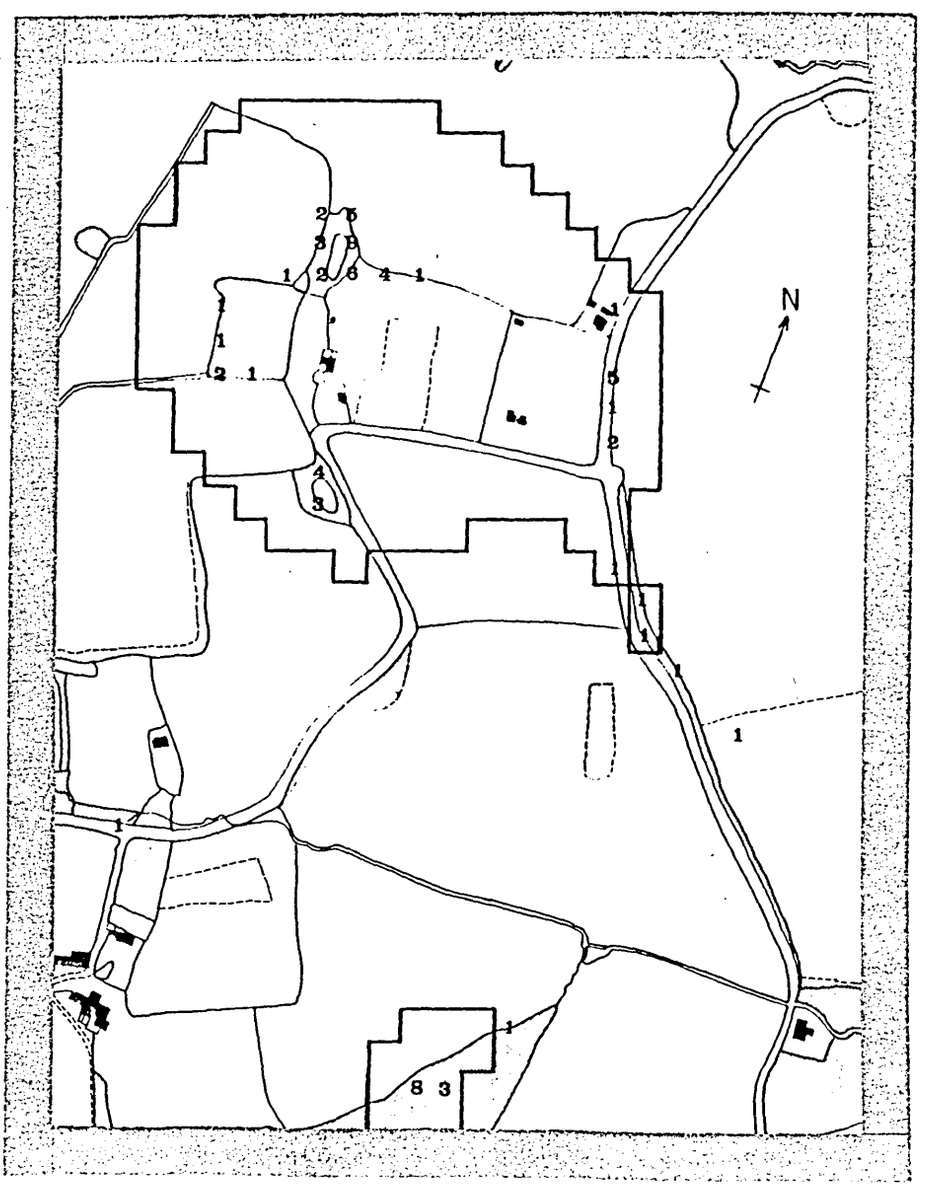
Bird 3
All data



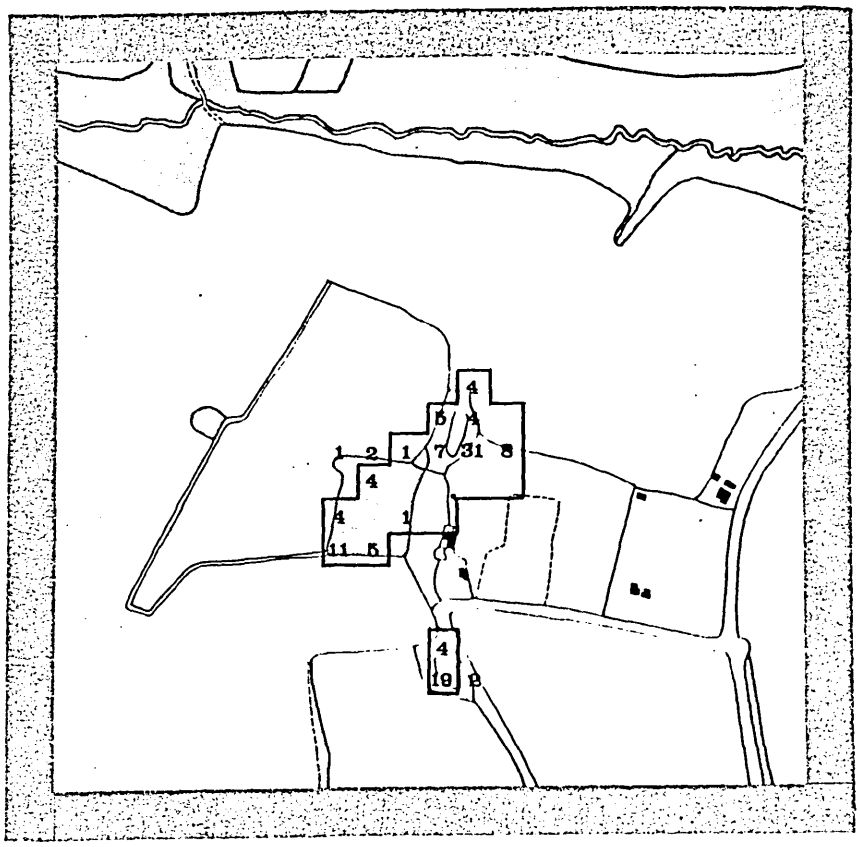
Bird 4



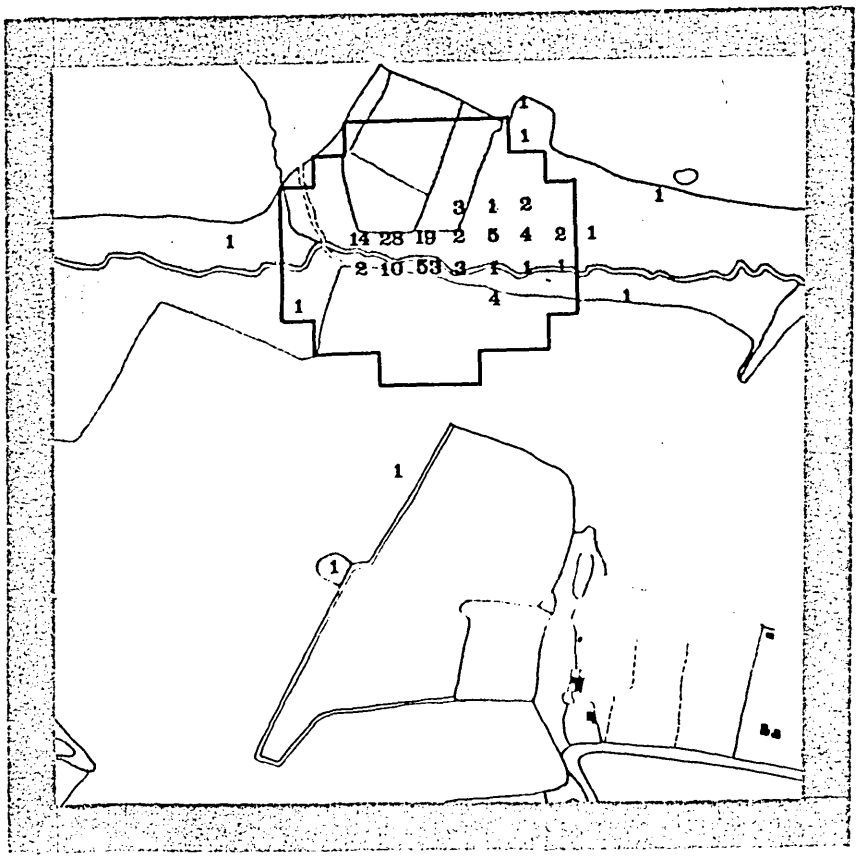
Bird 5



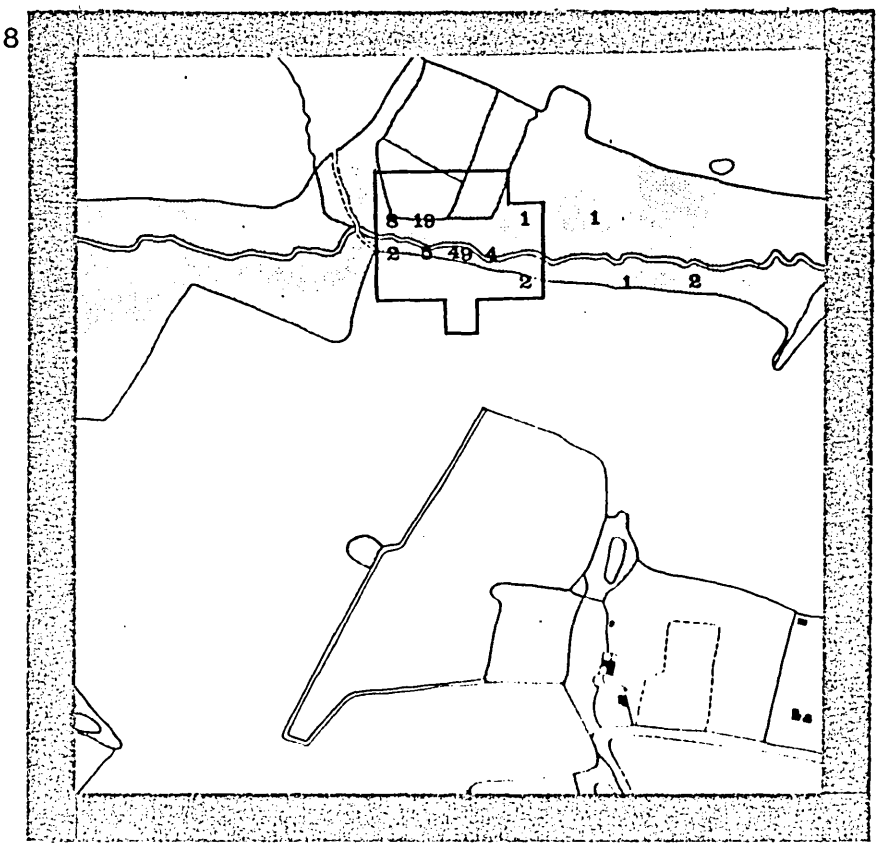
Bird 6


4
5 4
1 2 1 7 31 8
4
4 1
11 5
4
19 2

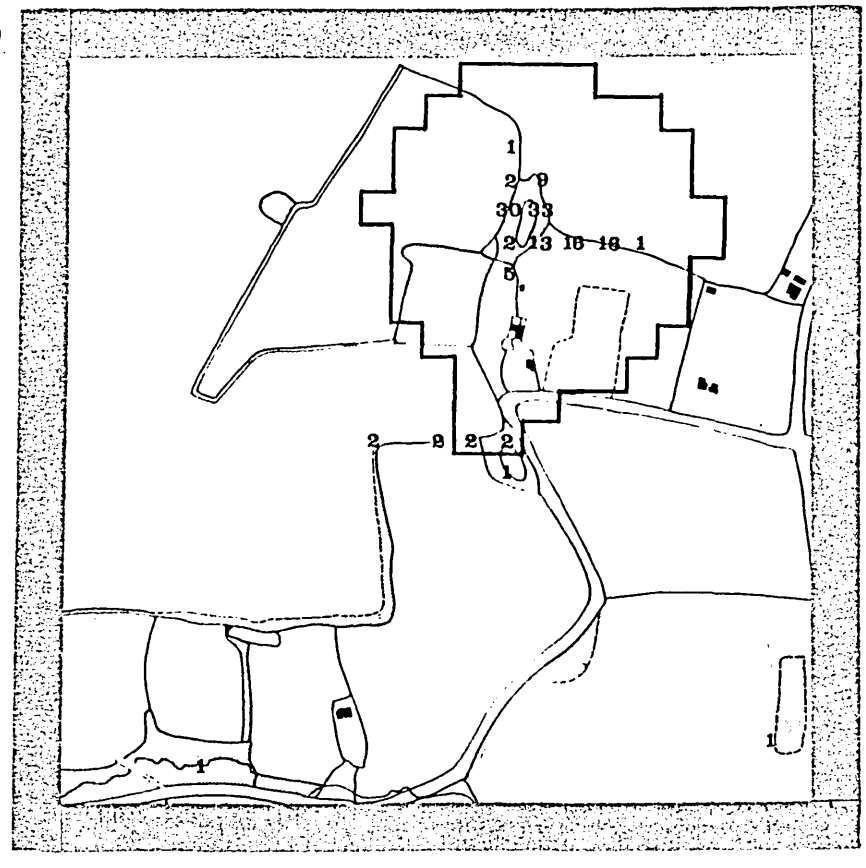
Bird 7


1
1
1
3 1 2
1 14 28 19 2 5 4 2 1
2 10 53 3 1 1 1
4 1
1
1
1

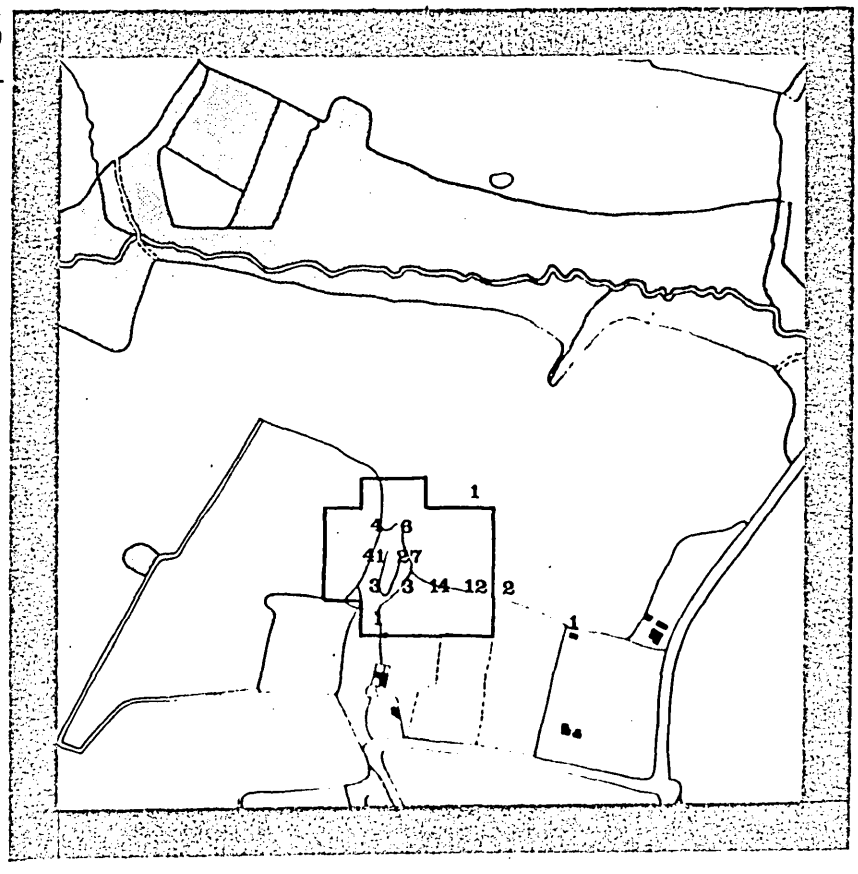
Bird 8



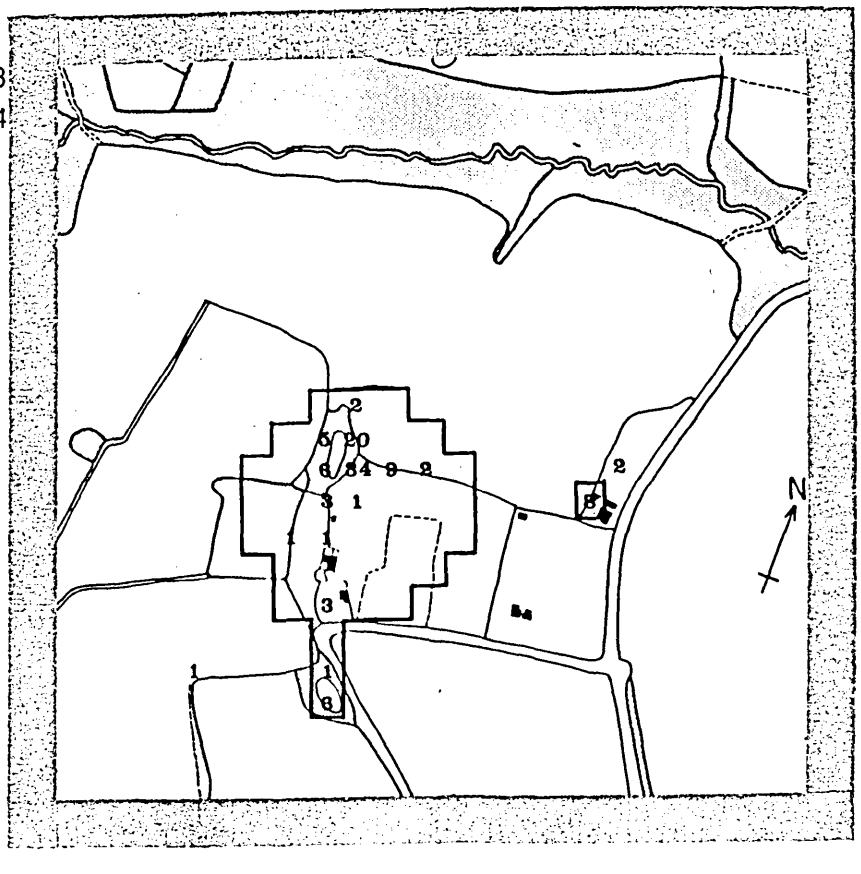
Bird 9



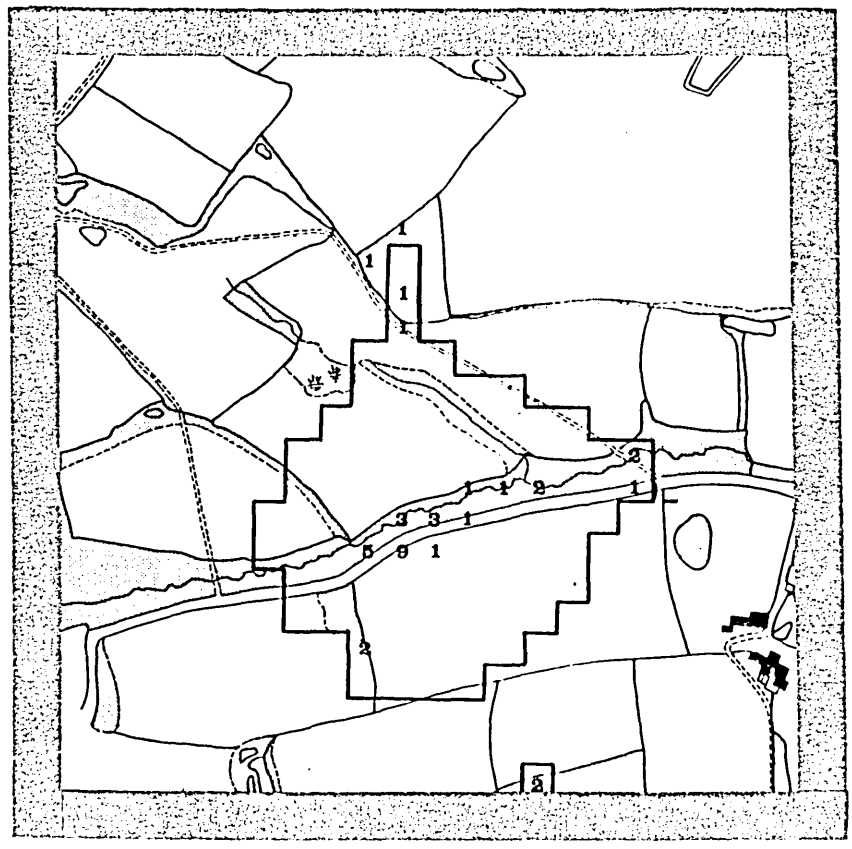
Bird 10
3-22 Mar
1983



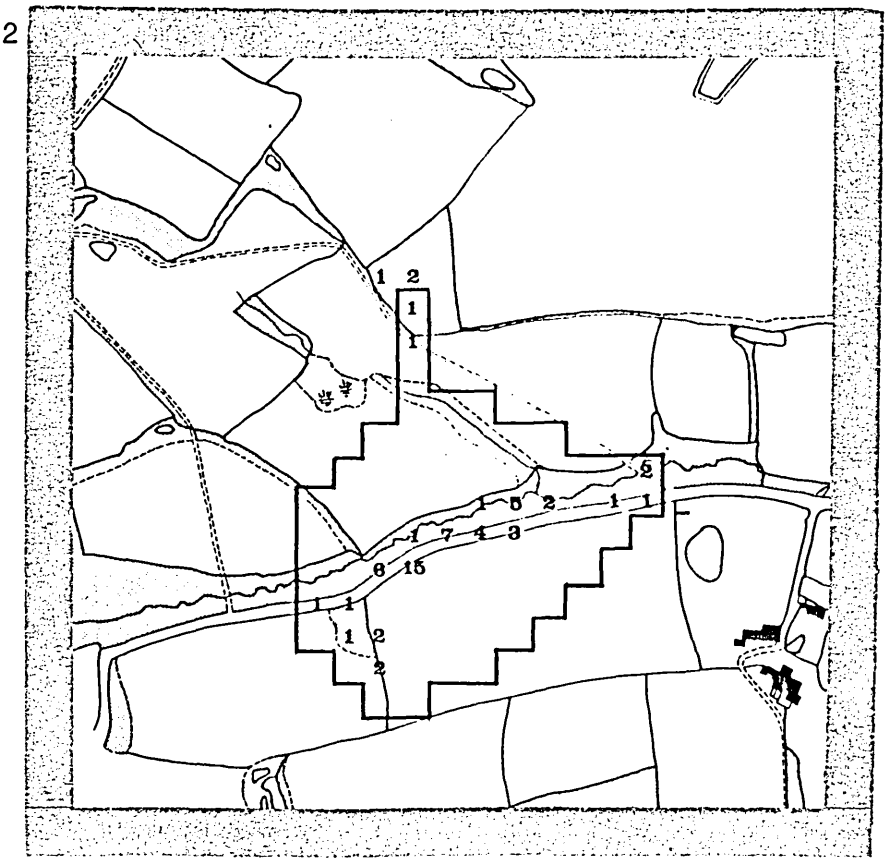
Bird 10
24 Nov 1983
- 24 Feb 1984



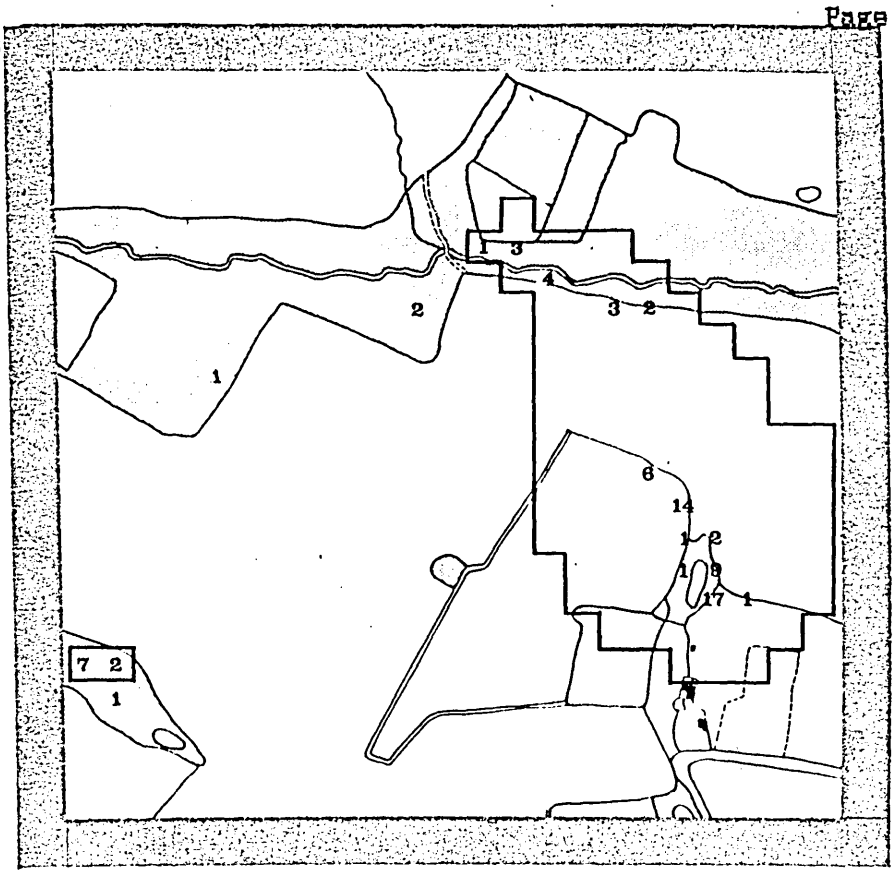
Bird 11



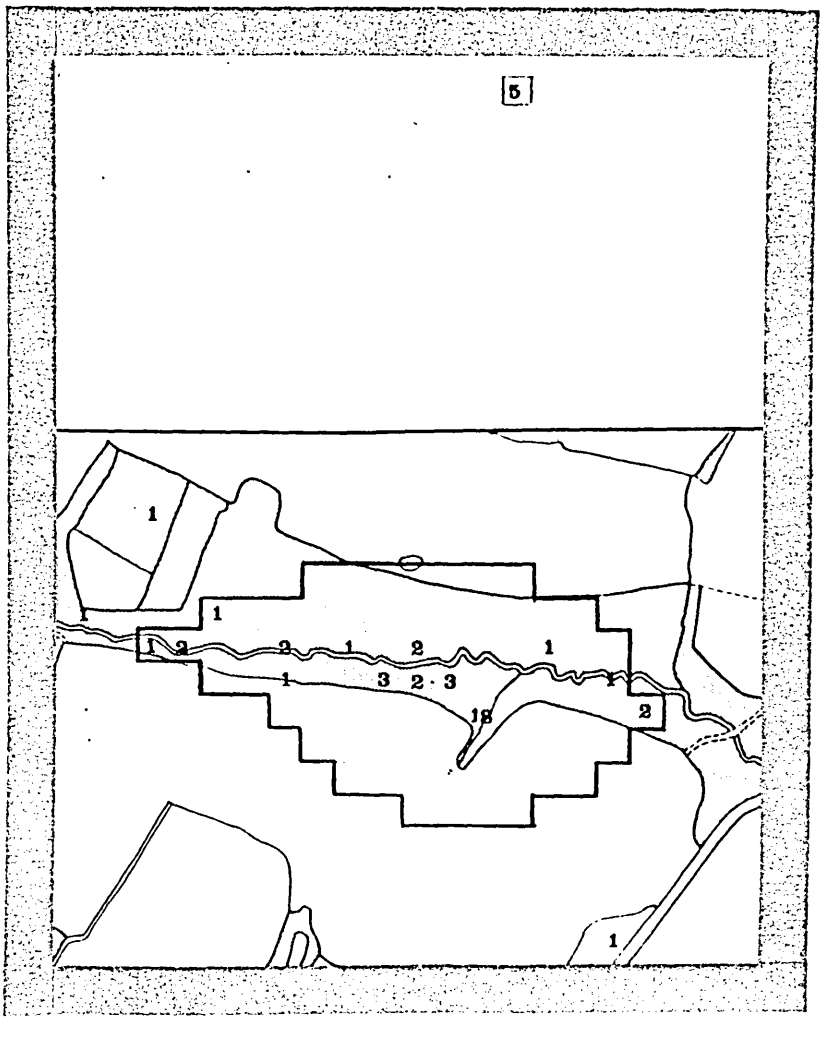
Bird 12



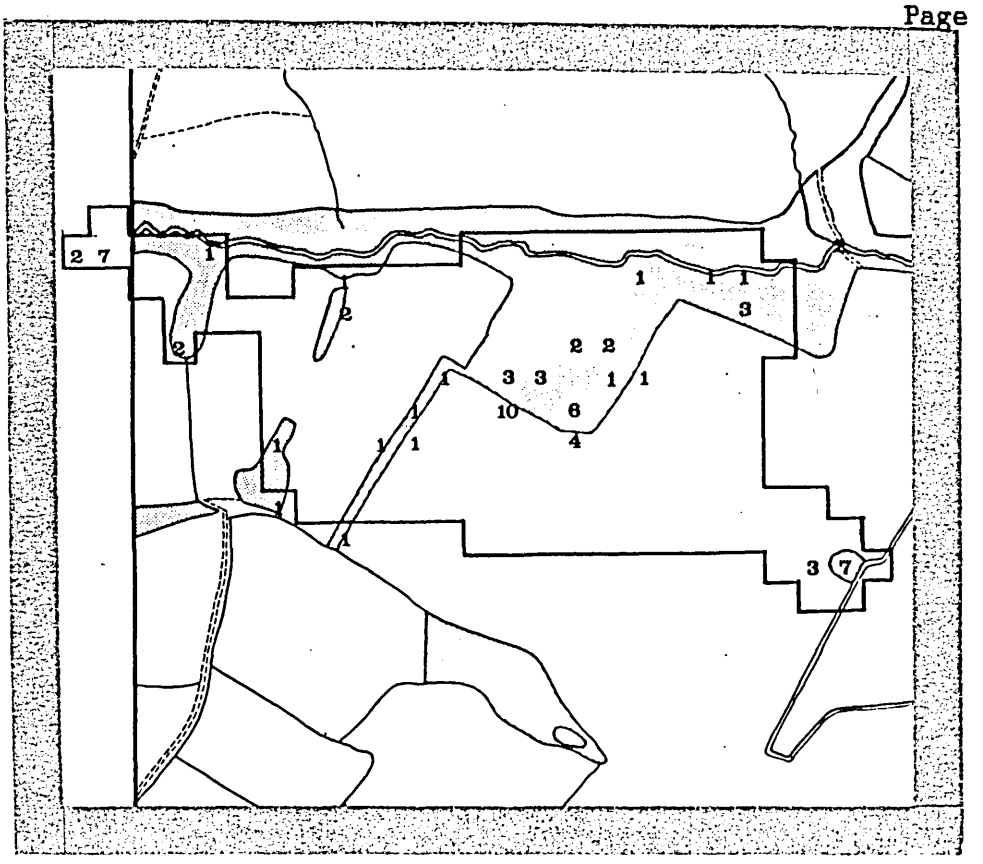
Bird 13



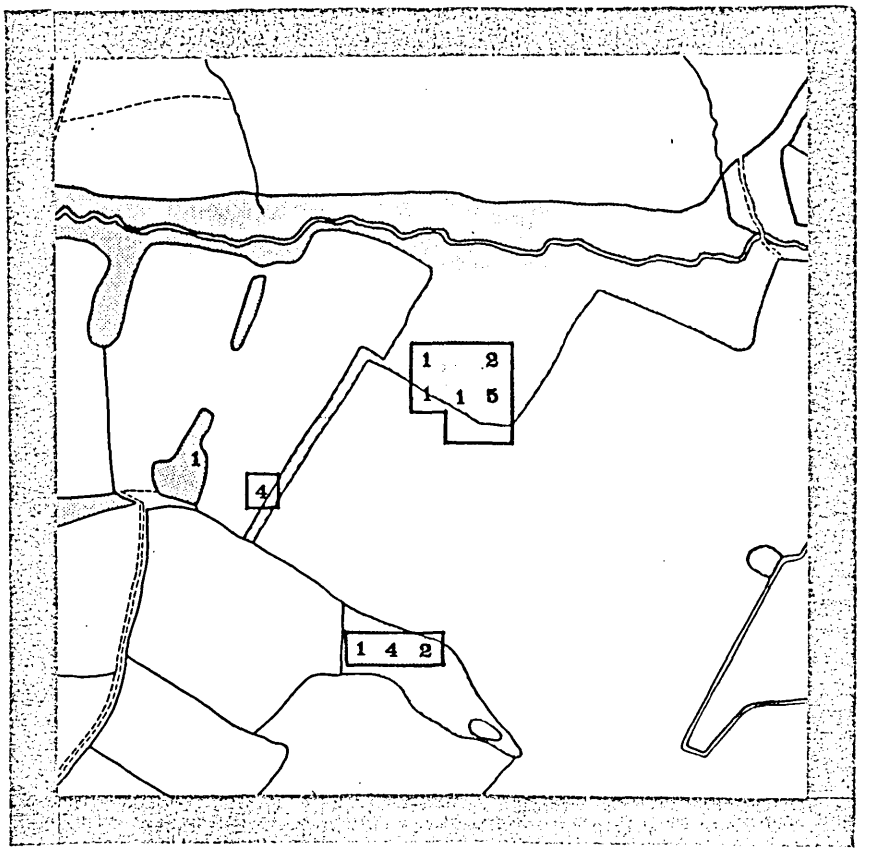
Bird 14



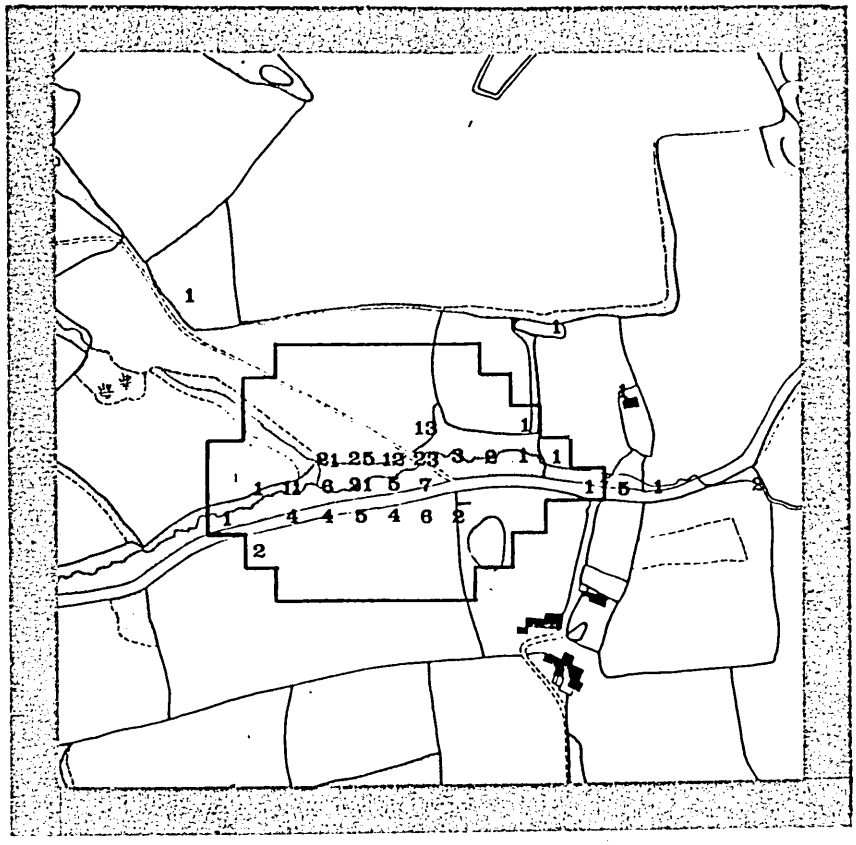
Bird 15



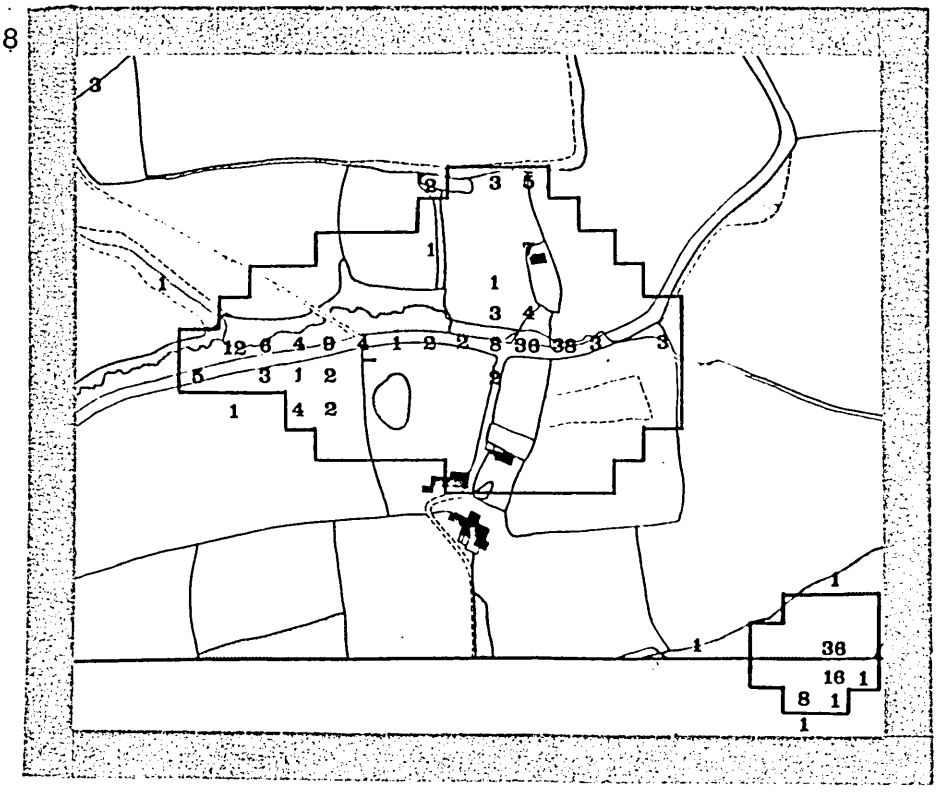
Bird 16



Bird 17



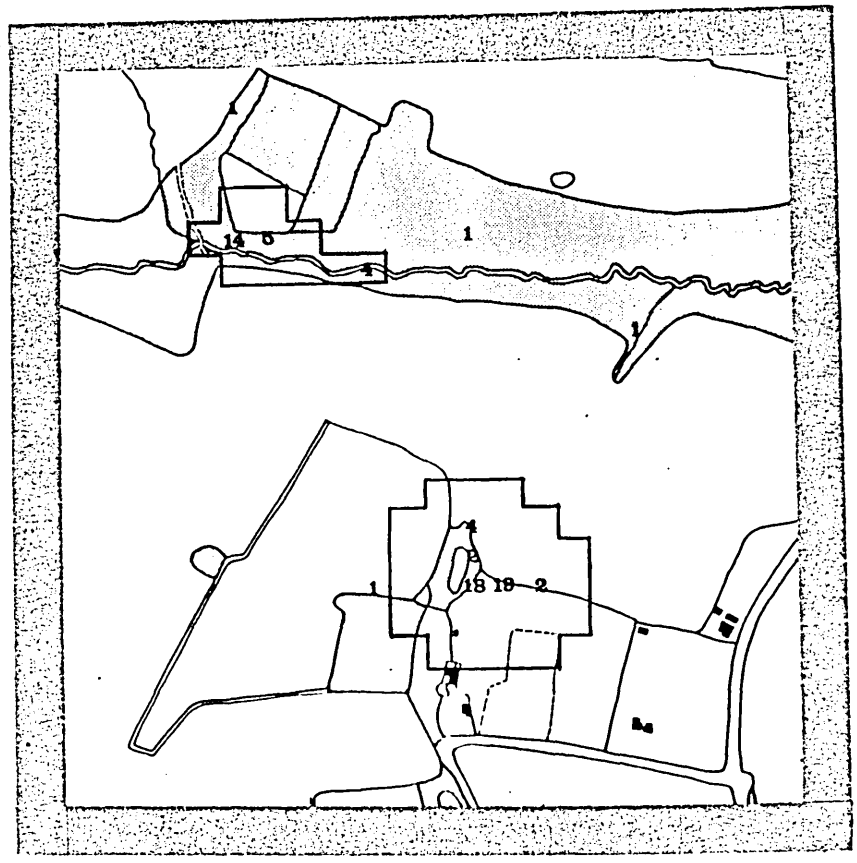
Bird 18



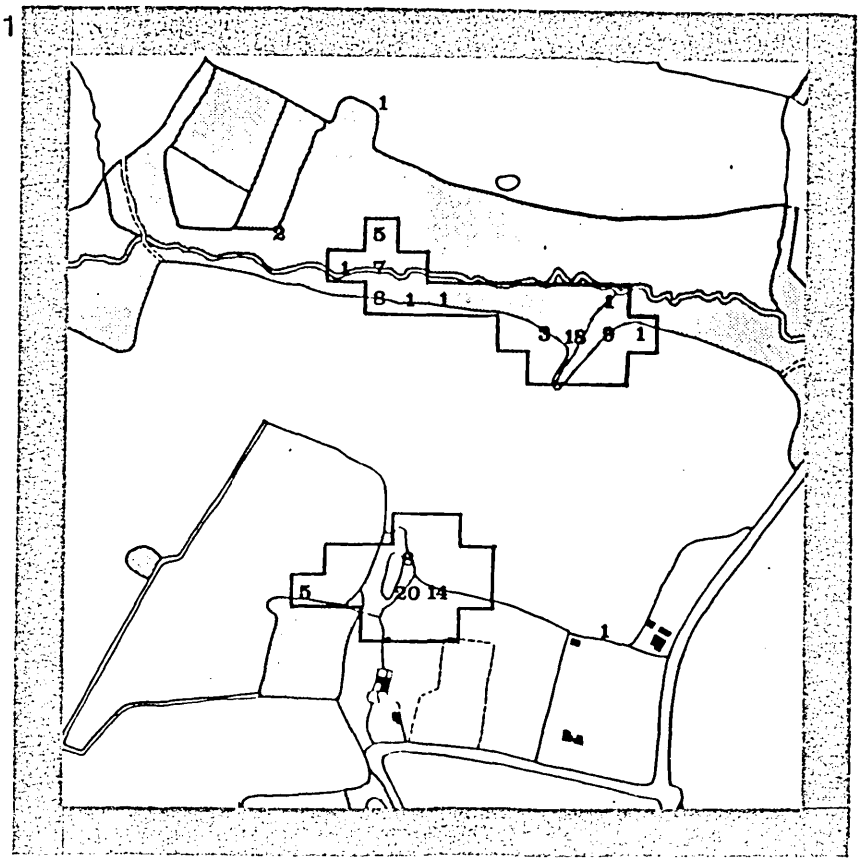
Bird 19



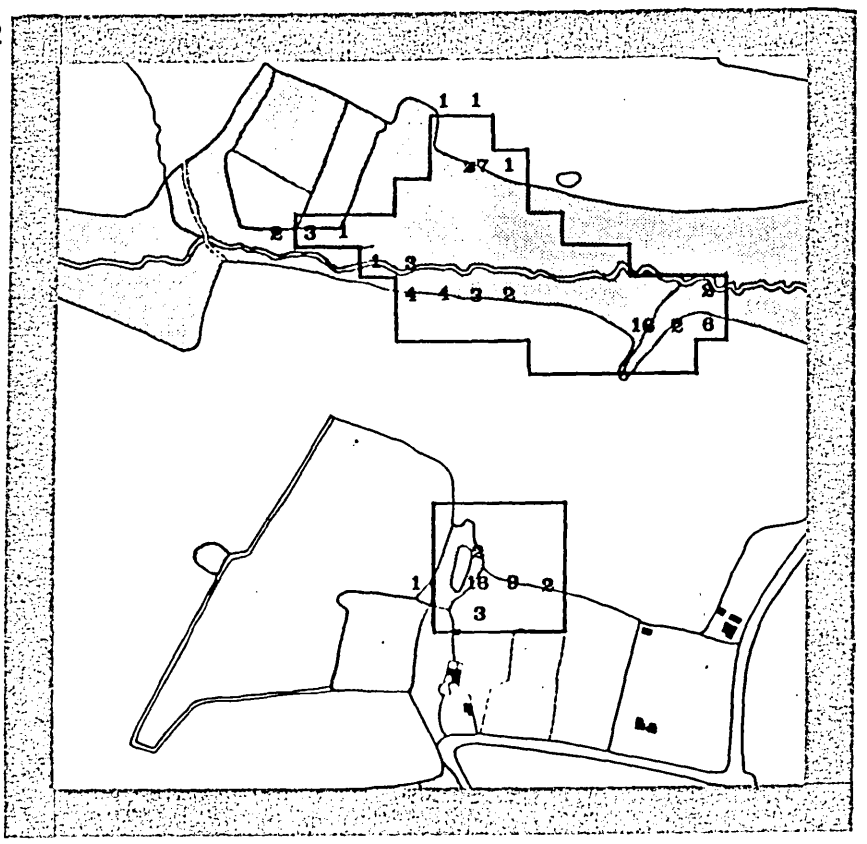
Bird 20



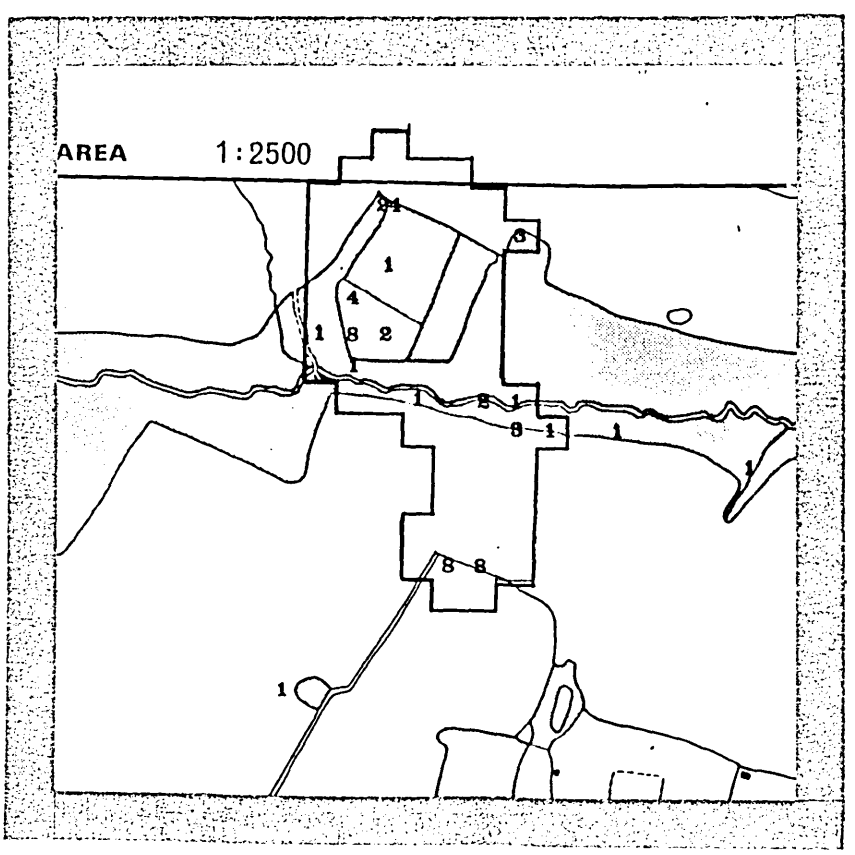
Bird 21



Bird 22



Bird 23



Chapter 2

Telling a good seed from a bad seed

1. INTRODUCTION

There is now plenty of evidence, from field and laboratory studies, of birds' abilities to forage economically (see Pyke et al., 1977; Krebs et al., 1983 for reviews). Given enough experience of the nutritional contents, handling times and abundance of different food items, birds will often select a diet consisting of the most profitable items; profitability being measured as the benefit of the food divided by the cost of finding, chasing, catching, subduing, consuming, digesting or otherwise handling it. The benefit of a food item is usually simplified to its energy value (E) which in turn is simplified to its weight. Cost is usually simplified to handling time (H). Profitability therefore, generally means the rate of energy intake (E/H). These simplifications are not always justified. Goss-Custard (1977a, b), for example, found that while redshanks (*Tringa totanus*) ate the largest of the polychaete worms available to them, their preferred prey was *Corophium*, a less profitable prey species. Royama (1970) using great tits (*Parus major*), Tinbergen (1981) using starlings (*Sturnus vulagaris*), and Stamps et al. (1981) using lizards (*Anolis aenus*) also present counter-examples to the energy maximisation assumption. Nevertheless, the profitability index E/H has been found useful in many studies.

Fewer studies, however, have attempted to discover how animals assess profitability. Hughes' (1979) argument that "recognition time" is an important cost in foraging decisions suggests that assessment may not be a simple matter. In laboratory environments, animals are often presented with a clear choice between large or small prey (e.g. Krebs et al., 1977; Gibson, 1980; and Barnard and Brown 1981). In the wild, prey which differ very obviously in size are likely to belong to different species, and thus inhabit different locations, contain different nutrients and require different hunting tactics. It is unlikely that a simple profitability index such as E/H would fully explain foraging decisions under these conditions. Even when E/H is appropriate, it may yet be a problematical measure of profitability. Where an animal is choosing items within a single prey type, they will vary over a continuous size range, not only in weight but also

in shape, which may affect their ease of handling. This is especially true when one considers that the energy content and handling time of a food item may be known for certain only after that item has been handled and consumed. An animal choosing between alternative items must rely on proximate cues such as size and shape. Its confidence in these cues will depend on the strength of their correlation with realised profitability.

The experiment described here, examines the selection of sunflower fruits by bullfinches. It is part of larger study (Greig-Smith and Crocker, 1986) in which food preferences were investigated when sunflower fruits were presented singly, in pairs and in groups. Sunflower fruits were used because they are large, variable in size and shape, easy to measure and weigh, and because the birds liked them. (In the wild, bullfinches feed on ash keys, which are about the same size as sunflower seeds, but in the laboratory ash keys were often refused.) In this experiment, fruits were offered in pairs and the bird was allowed to take only one of them. The aim was to discover whether acceptance or rejection of a fruit could be predicted from its shape or size and whether bullfinches preferred the fruit which, from proximate cues, was likely to be the more profitable of the pair. Previously, my supervisor, P. Greig-Smith, had conducted a similar experiment on nine birds. I extended this experiment, with a number of improvements in design (discussed in the Method) to a further three birds, and these form the subject matter of this chapter. A comparison of their behaviour with that of the earlier nine birds is made in the appendix to this chapter.

The proximate cues deemed to be important were weight, length, breadth and thickness of fruits; features such as colour and pattern were assumed to be irrelevant. To discover whether bullfinches preferred some kinds of sunflower fruits over others, size and shape features of individual fruits were entered into a stepwise linear discriminant analysis (Nie et al., 1975). By selecting and weighting the various measures, the program (DISCRIMINANT) produces the best linear function that will separate accepted from rejected fruits. A successful analysis of this sort enables one to predict (with a specified degree of confidence) whether a given seed will be rejected or accepted. It enables one to make statements like "Bird X prefers long, thin fruits more than short, fat ones." Each fruit may be placed along a linear discriminant function, its position indicating the likelihood that it will be chosen. The discriminant function may be interpreted as a preference scale, and each fruit's "score" can be

correlated with its prospective profitability to see whether preferred fruits were also likely to be the most profitable. Prospective profitability was estimated from multiple regression analyses described in the Method.

2. METHOD

The behaviour of three wild-caught bullfinches (one male and two females) is described here. They had been kept in outdoor aviaries for several months before trials began and maintained on a diet of sunflower (*Helianthus annus*), hemp (*Cannabis sativa*), rape (*Brassica napus*), canary grass (*Phalaris canariensis*), millet (*Panicum miliaceum*), and teasel (*Dipsacus fullonum*) seeds. Sunflower seeds were the largest and were preferred over the others. Thus when birds were required to choose between pairs of sunflower fruits in the experimental trials, they were already used to dehusking them and well-acquainted with the food content, and the handling times associated with fruits of different sizes.

2.a. Apparatus and procedure

Birds were tested individually in a cage measuring 1x1x1 m, containing perches and a water dispenser. Having been deprived of food overnight, they were presented with pairs of individually numbered, weighed and measured sunflower fruits in a shallow trough. They were allowed to inspect or handle either or both of the fruits before committing themselves to one of them, after which the trough was inverted removing the rejected fruit(s). After a seed had been successfully handled and eaten, or unsuccessfully handled and dropped out of reach through the barred floor, a six minute delay was imposed before another pair of fruits was presented. In earlier experiments (Greig-Smith and Crocker, 1986) a new pair was presented as soon as a bird had dropped or eaten a fruit. A delay was imposed in this experiment in order to discourage birds from "deliberately" dropping difficult fruits and hastening the next choice trial. Such a tactic would distort the data on the relationship between handling times and fruit sizes. (For birds 39 and 45, the results suggest that fruits were not being deliberately dropped, since the handling times

for seeds which were eventually dropped were longer on average than those for successfully handled fruits.)

Another innovation was that fruits which had been rejected in early trials were re-used in later trials so that handling times could eventually be obtained for both the accepted and the rejected fruits of a pair. This meant that prospective profitabilities based on proximate cues (weight and shape of fruits) could be compared with the realised profitabilities of the same fruits. It allowed me to compare realised profitabilities and shape characteristics of fruits that had been accepted on the first presentation with those accepted only on the second or subsequent presentations. Furthermore, as birds in these experiments received more than 150 pairs of fruits to choose from, the data set was large enough to estimate food handling costs for each bird individually.

From a hide, I recorded the time spent handling fruits until they were eaten or dropped. I also noted whether both fruits of a pair were "sampled" before one was chosen. Sessions were conducted daily and lasted for up to three hours.

2.b. The energy content of sunflower fruits

The energy content (E) of a fruit was assumed to be directly equivalent to the weight of its seed kernel (W_s), which was closely related to the unhusked fruit weight (W_f) and shape. Each sunflower fruit was measured for length, breadth and thickness to the nearest 0.1 mm and weighed to the nearest 1 mg. The relationship between the weight of a sunflower fruit, together with its dimensions, and the weight of the seed it contained was derived empirically from measurements of 200 fruits and their seeds (Greig-Smith and Crocker, 1986),

$$W_s = 0.59.W_f - 3.33.B - 1.50.T + 24.2 \quad (1)$$

where B is breadth and T is thickness. This equation, arrived at through stepwise multiple regression (Nie et al., 1975), accounted for 91% of the variation in seed weight ($F=637$, $df=3, 196$, $p<0.001$). Fruit weight alone was almost as good a predictor of seed weight, accounting for 88% of the variance ($r=0.94$, $p<0.001$, see Fig. 1). Length, breadth and thickness accounted, respectively, for 34% ($r=0.58$), 50% ($r=0.71$) and 48% ($r=0.69$) of the variance in seed weight, all significant at $p<0.001$. Birds could therefore use any or all of these cues to arrive at a good estimate of the

size of a seed contained within a sunflower fruit, without actually removing the fruit coat.

2.c. Handling costs

The handling cost (H) of a fruit was assumed to be directly equivalent to the time taken to crack open the husk and eat the seed inside, and was measured for each of the fruits chosen. From these data and the measurements of length, breadth, thickness and weight of sunflower fruits, stepwise multiple regressions were used to arrive at general equations predicting handling times. These were performed separately for each bird and are discussed in the results.

2.d. Profitability

The profitability of a food item is generally taken to be its energy content (E) divided by its handling cost (H) (see Krebs and McCleery, 1984). However, in these experiments, fruits were often dropped in the course of handling, and since the floor was barred they fell out of reach. In choosing between a pair of fruits it should profit a bird to estimate not only their energy contents and handling costs, but also the probability of accidentally dropping them. The prospective value of fruits was therefore calculated as,

$$V = \frac{W_e.(1 - P_d)}{(P_d).(T_d) + (1 - P_d).(T_h)} \qquad (2)$$

where P_d is the probability of dropping fruits and T_d is the time spent handling a fruit which was eventually dropped. As with handling times (T_h), a multiple regression of "dropping" times (T_d) was performed on fruit weight and shape characteristics in order to derive a general predictive relationship. The probability of dropping a fruit (P_d) was estimated by performing a stepwise linear discriminant analysis on fruit weight and shape characteristics to separate dropped fruits from successfully handled fruits.

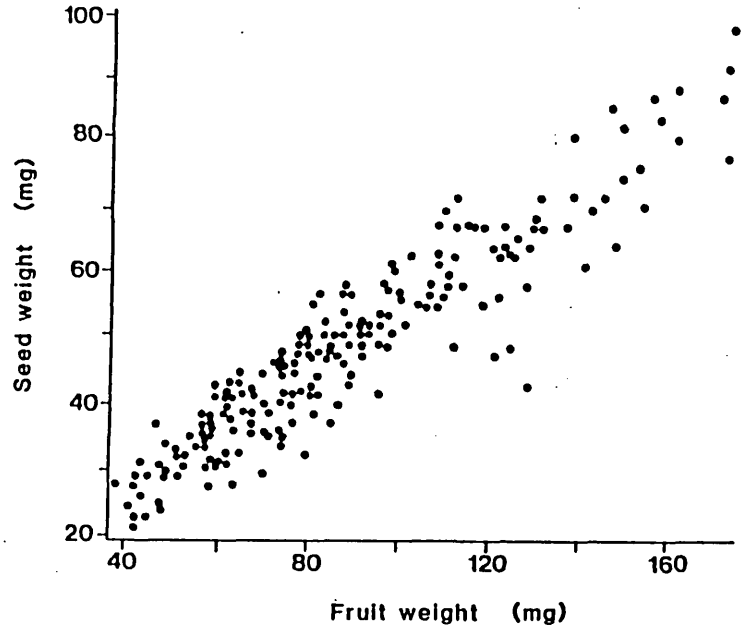


Fig. 1

Correlation between fruit weight and seed weight for 200 sunflower fruits: $r=0.94$, $p<0.001$ (From Greig-Smith and Crocker, 1986)

3. RESULTS

It was shown in the methods section that the weight of a sunflower seed, and hence its energy content, could be very accurately estimated from the weight and shape of the unhusked fruit (equation (1)). However, if birds are to estimate the prospective profitability of a fruit, they must also be able to judge how long it will take to dehusk it and, in these experiments, the likelihood of dropping it.

Figure 2 shows that as fruit weight increases, so does handling time ($r=.45$, $p<0.001$). It is also clear, however, that the variation in handling time also increases with fruit weight. In the multiple regression procedure, handling times and dropping times were therefore transformed using natural logarithms. The following relationships were obtained,

Bird 39

$$\ln(T_h) = .023W_f - .169L + .176L/T + 4.48 \quad (3)$$
($r^2=.44$, $F=27.8$, $df=3,107$, $p<0.001$)

$$\ln(T_d) = .45B + 1.021 \quad (4)$$
($r^2=.14$, $F=6.7$, $df=1,40$, $p=0.013$)

Bird 45

$$\ln(T_h) = .026W_f - .334T + 3.88 \quad (5)$$
($r^2=.46$, $F=51.1$, $df=2,118$, $p<0.001$)

$$\ln(T_d) = .149L + 2.48 \quad (6)$$
($r^2=.07$, $F=2.4$, $df=1,31$, $p=0.13$ ns)

Bird 48

$$\ln(T_h) = .019W_f + .194B + 2.33 \quad (7)$$
($r^2=.49$, $F=32.7$, $df=2,69$, $p<0.001$)

$$\ln(T_d) = .842L/B + 2.5 \quad (8)$$
($r^2=.10$, $F=7.7$, $df=1,72$, $p=0.007$)

where L=length, B=breadth, T=thickness, L/B=length to breadth ratio, etc.

Although these relationships are nearly all significant, the amount of variance in handling or dropping times that they explain is rather low. This means that bullfinches would be able to judge handling times from fruit size with very little certainty.

From discriminant analyses attempting to distinguish dropped fruits from those successfully handled and eaten, it was found that fruit weight was the major contributor to the discrimination function in each case (Table 1). As with handling and dropping times, the probability of

dropping a fruit (P_d) increased with fruit weight (Fig. 3). (For details of how P_d is derived from the discriminant function, see Norusis 1984.)

The principle finding of these analyses is that heavier sunflower fruits contain heavier seeds but they take longer to dehusk and are more likely to be dropped.

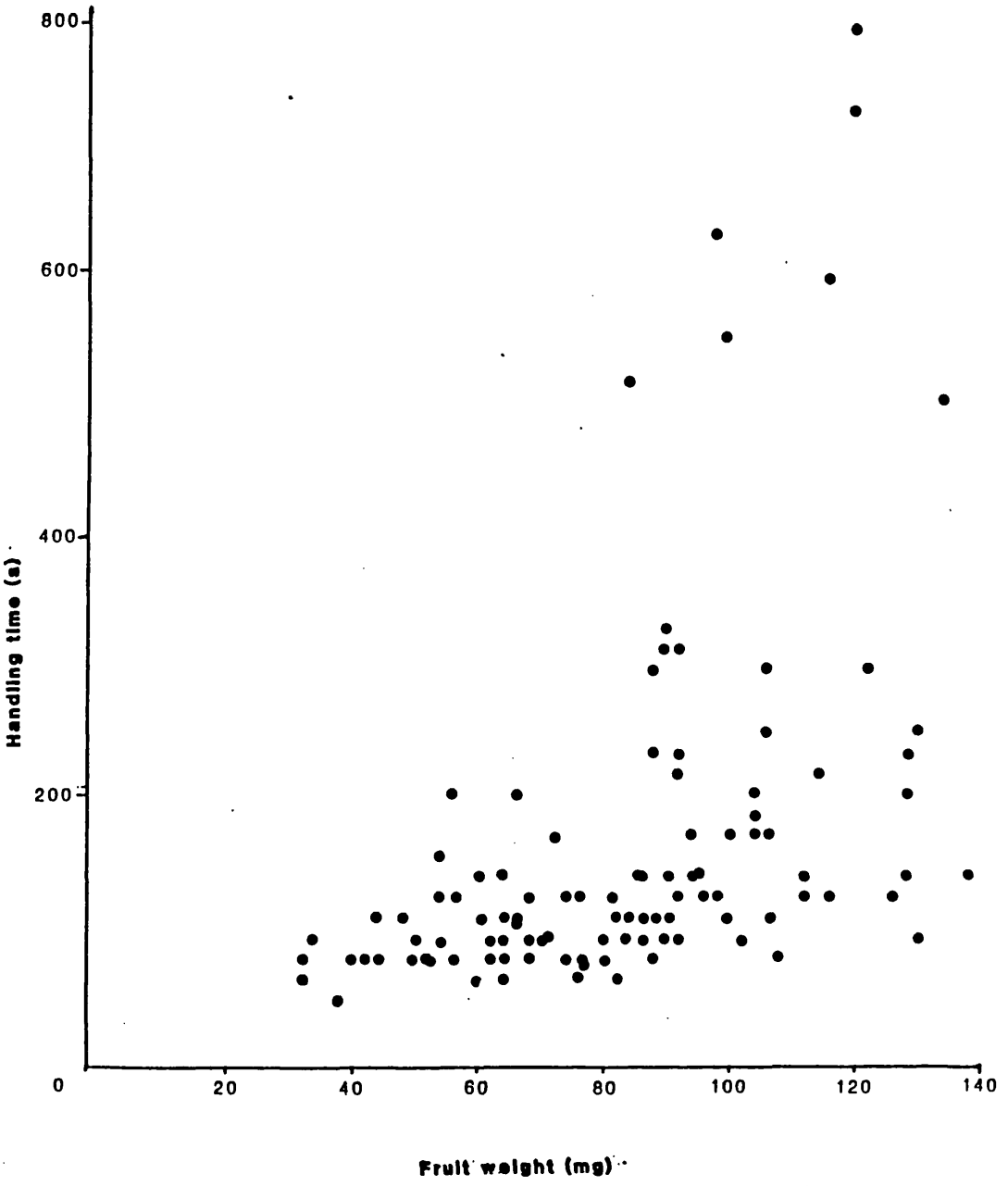


Fig. 2

Relationship between the weight of sunflower fruits and the time taken by bird 39 to remove their husks.

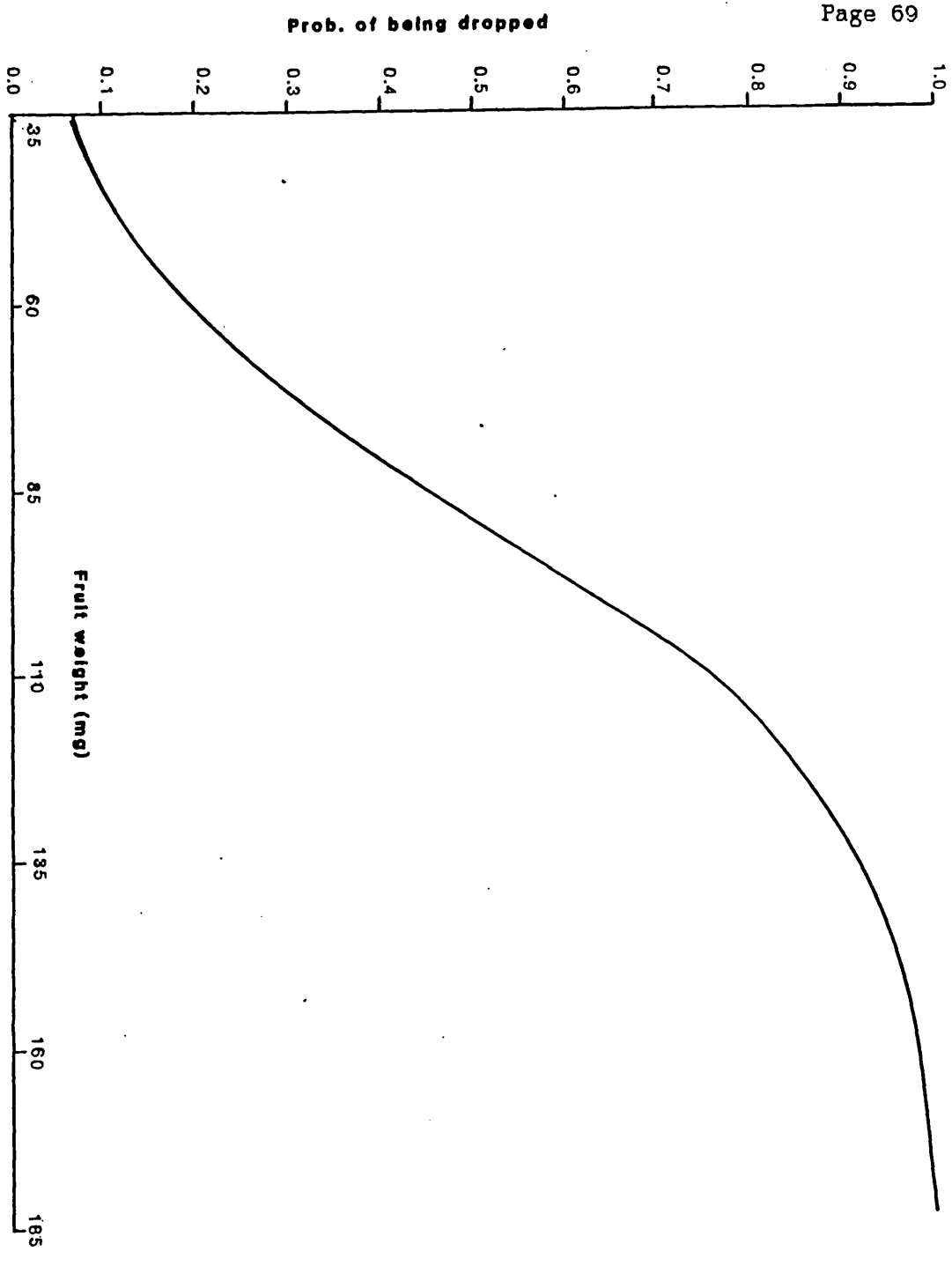


Fig. 3

Probability of a fruit being dropped plotted against fruit weight.

Table 1. Discriminant analyses on handled versus dropped fruits.

Bird	Significance of discrimination	Significant variables
39	χ^2=32.5***	W_f***, L/Th*
45	χ^2=32.9***	W_f***, L*
48	χ^2=42.0***	W_f***

*** p<0.001 ** p<0.01 * p<0.05

Table 2. Discriminant analyses on accepted versus rejected fruits based on absolute and relative measurements of seeds presented once only.

			Correlations between discriminant scores and					
Bird	Significance of discrim.	Contributing variables	Seed wght	Hand. time	P_d	Prosp. E/H	V	Real. prof.
39	χ^2=12.0***	R-thick.***	-.30	-.37	-.19	.34	.35	.14
45	χ^2= 6.3*	R-W_f (ns) R-breadth (ns)	-.62	-.50	-.53	.38	.40	.11
48	χ^2=65.6***	R-thick*** R-breadth***	-.48	-.60	-.57	.69	.62	.23

*** p<0.001 ** p<0.01 * p<0.05 R indicates a relative value (i.e. deviation from the other of the pair).

Table 3. Number of fruits presented, eaten, dropped or refused

Bird	Sex	Total	No. of fruits Dropped	Eaten	Refused	% trials in which both fruits sampled
39	F	160	42	111	7	21%
45	M	156	33	121	2	2%
48	F	158	74	72	12	58%

Table 4. Discriminant analyses on accepted versus rejected fruits based on relative measurements and including seeds which have been rejected in earlier trials.

Bird	Significance of discrim.	Contributing variables	Correlations between discriminant scores and Rel. seed wght	Rel. hand. time	Rel. prosp. E/H	Rel. real. prof.
39	χ^2=24.7***	R-thick.***	-.70	-.53	.30	.30
45	χ^2=10.1**	R-W_f**	-.96	-.86	.88	.36
48	χ^2=140.7***	R-thick*** R-W_f*** R-L***	-.65	-.42	.36	.36

*** p<0.001 ** p<0.01 * p<0.05 R indicates a relative value (i.e. deviation from the other of the pair).

Table 2 shows the results of discriminant analyses attempting to separate the accepted seeds from the rejected seeds with which they were paired. Significant discriminations were achieved for all birds, although for bird 45 no single dimension contributed significantly to the general equation. In each case, relative (i.e. differences between the fruits in a pair) rather than absolute measurements contributed most to the discriminant function. This suggests that birds made direct comparisons between the seeds in a pair. Bird 48 was the most discriminating individual, and was also the bird which most often (58% of trials) tested both fruits before selecting one of them (Table 3). Bird 45 was the least discriminating and the least likely to sample both fruits (2% of trials).

For each of the birds, the discriminant function -- a measure of preference -- was negatively correlated with seed weight, handling time and probability of dropping; and positively correlated with each of the three measures of profitability -- prospective E/H, V and realised profitability. (Significance levels are not appropriate for these correlations because the measures are all based on seed weight, and the discriminant function is also derived from this measure.) Discriminant scores were better correlated with the prospective measures of profitability (E/H and V) than with realised profitability. This is evidence that bullfinches chose fruits according to size and shape and did

not have access to other cues which I had overlooked. It also confirms the fact that profitability is difficult to predict from proximate cues.

The profitability measure V took account of the probability of dropping fruits, while E/H did not. Yet both measures were similarly correlated with the preference measure. It seems that birds' chose fruits without heed to the likelihood of dropping them.

Table 4 presents the same data as Table 3 but it makes use of additional data on birds' choices between fruits that they had rejected in earlier trials. When the birds had experienced all 80 fruit pairs, the rejected fruits were re-used in a further series of 40 or so trials and the rejected seeds from these trials used to make another 20 or so fruit pairs, and so on. Because birds met some fruits more than once, absolute measures were omitted and only relative measures entered into the analysis. Similarly, for discriminant scores based on *relative* measures, it is more reasonable to correlate them with *relative* measures of seed weight, handling time and profitability. Again, all three birds showed significant discriminations, and they paid most attention to fruit thickness and weight.

Tables 3 and 4 both show that the birds preferred thinner, lighter fruits, which are those most likely to be profitable. It has yet to be shown that the fruits they ate were in fact more profitable than those that they rejected. Table 5 shows how often birds chose the more profitable fruit of the pair. (Cases were omitted where both fruits of a pair were dropped and whose profitabilities were hence zero.) It may be seen that all birds tended to choose the more profitable fruit and that this tendency was greatest for bird 48 which was most discriminating according to the above analyses. Bird 45 was the least discriminating of the three and showed only a weak tendency to pick the most profitable fruit. Similarly, Table 6 presents the results of Kruskal-Wallis tests comparing the shapes and profitabilities of fruits which were accepted on the first presentation with those accepted on the second, third and later presentations. Again, it confirms that birds 39 and 48 were more likely to pick the thinner more profitable fruit of a pair. The thicker, less profitable fruits were accepted only on later trials.

Table 5. Prospective versus realised profitabilities.

Choices made	Bird 39	45	48
More profitable	81	75	57
Less profitable	35	66	11
Binomial probability	p<0.0001 z=4.4	p<0.25 z=0.67	p<0.0001 z=5.57

Table 6. Kruskal-Wallis tests comparing fruit size, shape and profitability of fruits accepted on first, second and later presentations.

variable	mean rank* of fruits accepted on presentation no. 1	2	≥3	χ^2	sig.
Bird 39					
thickness	65.2	75.4	90.1	7.8	p<0.05
profitability	81.5	64.7	61.2	7.1	p<0.05
Bird 45					
	no significant variables found				
Bird 48					
weight	61.4	64.8	107.4	30.0	p<0.001
thickness	60.2	70.0	105.0	27.1	p<0.001
breadth	59.6	70.2	105.8	28.6	p<0.001
profitability	83.9	77.9	44.5	23.9	p<0.001

* fruits are ranked in ascending order of thickness, profitability etc.

4. DISCUSSION

When presented with pairs of sunflower seeds, all three birds preferred fruits within a certain range of size and shape, which in turn was positively correlated with the fruits' prospective profitabilities. Two of the birds chose the more profitable fruit significantly more often than would be expected by chance. Relative measures of size and shape were better guides to the birds' choices than were absolute measures. This suggests that birds were actively comparing the alternatives before

deciding on one of them. Greig-Smith and Crocker (1986) found that birds were more selective when choosing fruits from a dish of 15 fruits, than they were when fruits were presented singly with short intervals between them. Similarly, Jaeger et al. (1982) found that when salamanders were able to see all the flies available to them, they attacked fewer small, unprofitable flies than they did when the same the same density of flies was visible only in ones and twos. (The implication is that salamanders use proximate visual cues, rather than the retrospective capture rate, to assess prey abundance.)

Although each of the birds dropped a high proportion of fruits chosen (21 to 50% of total fruits presented), I was unable to show that they took account of the probability of dropping a fruit when deciding which one to pick. The discriminant scores were negatively correlated with P_d, as we would expect, but their correlation with the profitability index V (which takes account of P_d) was not very different to that with the simpler index E/H. Other experiments however (Greig-Smith, 1984 and Greig-Smith and Wilson, 1985) have shown that bullfinches can modify their behaviour in response to the costs of dropping fruit. In particular, birds have been shown to take longer to dehusk fruits when handling them over a barred rather than a solid floor. In the wild, bullfinches drop or discard many ash keys when feeding in the tree canopy and it is reasonable to suppose that the probability of being dropped is an important part of a fruit's prospective profitability.

It has been assumed in this chapter, and in the optimal foraging literature in general, that birds which are more discriminating and more likely to recognise the most profitable prey, will have a selective advantage over birds which make less wise choices. From the results of the experiment described here, we might expect bird 48 to be the most successful, and bird 45 the least successful forager. However, when we compare the birds' intake rates for those fruits which were eaten, we find that bird 48 was the least efficient feeder, managing to consume 0.16mg/s: bird 45 fed at 0.23mg/s and bird 39 at 0.28mg/s. When time wasted on dropped fruits is included, the order of feeding efficiency remains unchanged with the birds achieving 0.13mg/s (48), 0.18mg/s (45) and 0.19mg/s (39). Perhaps bird 39, being most efficient at removing the seed husks, did not "need" to discriminate very strongly between the different fruits. Whereas bird 48, being a relatively clumsy seed handler was obliged to consider their relative merits. Such an explanation would

imply that evolution has not selected animals to maximise the benefits and minimise the costs of a behaviour but rather to "satisfice" (Simon, 1956), to "do enough to get by" (Myers, 1983). Since evolution acts upon relative differences between individuals, an animal does not need to behave perfectly in order to gain a selective advantage over its competitors; it merely needs to behave better than them. Over many generations this may lead to a situation where most animals are acting close to the optimum, but it is equally possible that animals will arrive at different solutions to the same problem. Thus if bird 45's proficiency at cracking sunflower husks enables it to feed at a better than average rate, what incentive has it to further improve its performance by honing its discriminatory powers? According to Myers, "Satisficing predicts that animals should be riddled with behavioral traditions, drifting through routines that meet each requirement but optimize none. They will switch from their traditions only once they no longer work -- jerked out of complacency by the sudden appearance of a predator or cumulative deterioration in feeding conditions." Perhaps bird 45's failure to pick the most profitable sunflower fruits from the pairs on offer, was due less to its inefficiency than its complacency.

Appendix: Comparison of the behaviour of birds 39, 45, 48 with that of a larger group of birds which had undergone a similar experiment.

The behaviour of birds 39, 45 and 48 is more clearly understood in the context of a series of food selection experiments involving a larger subject group and reported in Greig-Smith and Crocker (1986). In particular, the experiment performed on the three birds described in this chapter was my modification of another experiment involving nine bullfinches carried out by P. Greig-Smith.

In the latter experiment, rejected fruits were not re-presented to the birds and therefore data on handling costs were available for only accepted fruits, that is, less than half the fruits actually presented. Data from individual birds was therefore combined in a single data set. Prospective handling times (T_h) and dropping times (T_d) were calculated from the same equations for each bird. The probability of a fruit being dropped (P_d) was also calculated from the combined data set. The following relationships were obtained.

$$\ln (T_h) = 0.03W_s + 0.51B/T + 2.14$$
$$(F=19.5,\ df=2,183,\ p<.001,\ r^2=0.17)$$

$$\ln (T_d) = 0.98B/T + 1.66$$
$$(F=4.0,\ df=1,22,\ p<.05,\ r^2=0.02)$$

where W_f stands for the weight of a sunflower fruit and W_s is the weight of the seed inside. B/T is the breadth to thickness ratio of a fruit.

Handling time (T_h) is most strongly related to seed weight (W_s) for these birds. Similarly, for birds 39, 45 and 48, equations (3), (5) and (7) show that handling times were best predicted by fruit weight (W_f). Fruit weight and seed weight are highly correlated (r=0.94, see Fig. 1) and since seed weight is not a true proximate cue (birds have direct access only to fruit weight), I omitted it as an independent variable in my analyses. Nevertheless, it appears that handling times could be predicted from similar characteristics both for my own group of three and the larger group of nine birds.

Equations predicting dropping times (T_d) showed more variation between birds but were all based on the shape of the fruits rather than

Table A1: Results of multiple regression analyses predicting handling times (T_h) and dropping times (T_d) from proximate cues, for birds 39, 45 and 48.

Bird 39

$$\ln(T_h) = .023W_r - .169L + .176L/T + 4.48 \quad (3)$$
(r^2=.44, F=27.8, df=3,107, p<0.001)

$$\ln(T_d) = .45B + 1.021 \quad (4)$$
(r^2=.14, F=6.7, df=1,40, p=0.013)

Bird 45

$$\ln(T_h) = .026W_r - .334T + 3.88 \quad (5)$$
(r^2=.46, F=51.1, df=2,118, p<0.001)

$$\ln(T_d) = .149L + 2.48 \quad (6)$$
(r^2=.07, F=2.4, df=1,31, p=0.13 ns)

Bird 48

$$\ln(T_h) = .019W_r + .194B + 2.33 \quad (7)$$
(r^2=.49, F=32.7, df=2,69, p<0.001)

$$\ln(T_d) = .842L/B + 2.5 \quad (8)$$
(r^2=.10, F=7.7, df=1,72, p=0.007)

where L=length, B=breadth, T=thickness, L/B=length to breadth ratio, etc.

their weights (equations 4, 6 and 8). The same was true of dropping times for the group of nine.

Another similarity between the two bird groups is that, although the equations predicting handling and dropping times were often highly significant, the amount of variance explained was quite low. 44-49% of variation in handling times was explained for birds 39, 45 and 48 while proximate cues could only explain 17% of the variation in handling times for the group of nine. Proximate cues could explain only 2-14% of the variation in dropping times. Birds in general would not have been able to use the shape or weight of sunflower seeds to judge with much certainty how long it would take to dehusk them.

For the group of nine, a discriminant analysis to separate dropped fruits from those which were successfully handled and eaten, showed fruit weight (W_f) to be the only important variable. The probability of dropping a fruit (P_d) was thus estimated as a simple linear function of W_f.

$P_d = 0.006W_f - 0.148$

Discriminant analyses performed on dropped vs. handled fruits for birds 39, 45 and 48 also showed W_f to be the most important variable in each case, although other variables had a significant influence (see Table 1). In reality, P_d is unlikely to take the form of a linear function -- such a function implies that very small fruits could have a negative probability of being dropped, while large fruits could have a P_d of more than 1. Obligingly, the SPSS* DISCRIMINANT package makes use of Bayes theorem to calculate a value for P_d (taking values between 0 and 1) directly from the discriminant scores (Norusis, 1984). When plotted against fruit weight this gives a sigmoid, rather than a straight line relationship (Fig. 3). This method of calculating P_d also takes into account the influence of variables measuring fruit shape as well as weight. For these reasons, P_d calculated for birds 39, 45 and 48 was derived from the discriminant scores, rather than fruit weights.

Table A2 shows the results of a discriminant analysis on accepted versus rejected fruits as they were reported in Greig-Smith and Crocker (1986). It also shows the re-analysis of birds 39, 45 and 48 (as presented in Table 2) incorporating the modifications discussed above. Comparing the data on birds 39, 45 and 48 in the published paper with the re-analysed data, it may be seen that the significance of the discriminations are very similar. Likewise, the correlations of the discriminant scores with seed weight, handling time, probability of dropping and E/H are not much

Table A2. Discriminant analyses on accepted versus rejected fruits based on absolute and relative measurements of fruits.

Data above the dotted line are as published in Greig-Smith and Crocker (1986). Data below the line are from Table 2 of this chapter and represent a re-analysis of the data for birds 39, 45 and 48 with the following differences: 1) The data set includes only those fruits presented for the first time, whereas Greig-Smith and Crocker (1986) also included some data on previously rejected fruits; 2) Seed Weight (W_s) was omitted from the analysis since, unlike fruit weight (W_f) it is not a true proximate cue; 3) The probability of dropping a fruit (P_d) was calculated from a discriminant analysis of dropped versus handled fruits, whereas Greig-Smith and Crocker (1986) used a linear function of fruit weight to estimate P_d.

Bird	Significance of discrim.	Contributing variables	Correlations between discriminant scores and: Seed wght	Hand. time	P_d	Prospective. E/H
34	χ^2=9,2**	R-breadth** A-breadth*	,59	,49	,75	,80
30	χ^2=3,9*	R-breadth*	,02	-,09	,04	-,33
33	χ^2=4,9*	A-W_s*	,10	,11	,11	,04
28	χ^2=7,0**	R-breadth/thickness**	-,05	-,05	,07	-,04
36	NS	---	---	---	---	---
26	χ^2=26,6***	A-W_s** A-length/breadth*** A-length***	,18	,22	,21	,29
22	NS	---	---	---	---	---
27	χ^2=7,2**	A-length/breadth**	,06	,04	,07	,12
39	χ^2=8,3**	R-thickness**	-,27	-,36	-,28	,18
45	χ^2=4,5*	R-W_s*	-,73	-,56	-,70	,64
48	χ^2=65,8***	R-W_f*** R-length*** A-length/thickness* A-thickness* A-length**	-,52	-,57	-,57	,50
39	χ^2=12,0***	R-thickness***	-,30	-,37	-,19	,34
45	χ^2= 6,3*	R-W_f (ns) R-breadth (ns)	-,62	-,50	-,53	,38
48	χ^2=65,6***	R-thickness*** R-breadth***	-,48	-,60	-,57	,69

*** p<0,001 ** p<0,01 * p<0,05 R indicates a relative value (i.e. deviation from the other of the pair).

changed. There are some differences in the significant variables entering the analyses. Relative thickness is the major contributing variable for bird 39 in both analyses. For bird 45, however, relative seed weight has been replaced by relative fruit weight as the major variable in the re-analysis. This is not surprising, since seed weight was omitted in the re-analysis and is highly correlated with fruit weight. For bird 39, relative fruit weight has been replaced by relative thickness as the most significant variable. Again this is not remarkable since weight, length, thickness and breadth are all closely correlated and slight differences in the data set may easily produce changes in the order in which variables are entered into the stepwise discriminant analysis.

The results from birds 39, 45 and 48 are generally more coherent than those from the larger group of eight (one bird was discarded because of insufficient data). Each of the former birds tended to use relative measures in deciding which fruit to pick, and to pick the relatively lighter fruit, with the shorter handling time, with the lower probability of being dropped and the higher prospective profitability. The behaviour of the larger group was more variable. Two birds (36 and 22) either failed to discriminate between fruits or else were using cues which we failed to measure. Bird 34 (and to a lesser extent bird 26) preferred fuits with heavy seeds, with longer handling times, higher prospective profitabilities but fruits that were also more likely to be dropped. For the remaining birds, correlations with the discriminant scores were all rather low except for bird 30 which appeared to prefer fruits with poor prospective profitabilities.

The variability in choice behaviour of the larger group may reflect a a genuine variability in the bullfinch population as a whole. Different birds may naturally adopt different strategies in food selection. Birds which are more skilled at dehusking fruits might attempt to maximise profitability by choosing those with large seeds, albeit with longer handling times. Others may try to improve profitability by choosing those fruits with the shorter handling times and less chance of being dropped, albeit containing smaller seeds. This seemed to be the strategy used by birds 39, 45 and 48, and remembering that these birds were obliged to wait at least six minutes between trials, then a cautious strategy might make sense. In another experiment (reported in Greig-Smith and Crocker, 1986) birds were allowed to choose between fruits presented singly with a fixed time gap between their appearance. For the five birds which made

significant discriminations between accepted and rejected fruits, the discriminant scores were all negatively correlated with seed weight, handling time and P_d; that is, like birds 39, 45 and 48 they preferred smaller fruits with shorter handling times and less likelihood of being dropped.

There is other evidence reported in Greig-Smith and Crocker (1986) which supports some of the conclusions made in this chapter.

It was noted that bird 48 which was the most discriminating individual was also the most likely to "sample" both fruits before making its final choice. Bird 45 hardly ever sampled both fruits and it was the least discriminating of the the three. Similarly, in the group of nine, sampling behaviour was inversely correlated with the probability of dropping fruits ($r=0.72$, $p<0.05$), suggesting that birds were actively comparing the members of each fruit pair.

By re-presenting previously rejected fruits to birds 39, 45 and 48, I was able to compare realised as well as prospective profitabilities. I was able to show that all three birds tended to choose the fruit with the higher realised profitability of the pairs presented (though this tendency was not significant for bird 45), but that the correlation with discriminant scores was higher for prospective than for realised profitabilities (Table 2). In the published paper, using the subset of fruits that were chosen and successfully handled by members of the larger group, and additional data from the experiment where fruits were presented singly, we made a similar comparison. In 11 out of 14 birds' preferences were more closely correlated with prospective rather than realised profitabilities.

Chapter 3

Telling a good patch from a bad patch

1. INTRODUCTION

The principal aims of this experiment were to investigate how well bullfinches are able to track changes in the quality of food patches, what cues they use in so doing, and what are the effects of previous experience.

In an experiment using titmice (*Parus* spp.) Smith and Sweatman (1974) (see also, Smith and Dawkins, 1971) presented captive birds with 6 food patches (cups) containing various densities of mealworms. The birds soon learned to concentrate on the cup containing most worms, but they continued to sample the other cups. When the experimenters gradually decreased the food density of the richest patch and increased that of the poorest (so that the erstwhile richest became the poorest and *vice versa*) birds responded by decreasing the time spent in what was the richest (now poorest) patch and concentrated their search efforts on what was (and still is) the second best patch. They did not discover that the orignally poorest patch was now the best. This result shows that birds can rank food patches according to relative food density, and remember that ranking at a later date. It also suggests that the birds' sampling strategies were not thorough enough in this case to make the best use of the changing circumstances.

Several authors (e.g. Oaten, 1977; Green, 1980; McNamara, 1982; Stephens and Charnov, 1982; Lima, 1983, 1984, 1985; Kacelnik and Krebs, 1985) have noted that in a stochastic environment, where food comes in discrete bits at irregular intervals, the quality of a particular patch is uncertain at the outset. The longer an animal feeds within a patch, the surer it becomes of its quality relative to other patches. As McNamara (1982) puts it, " because one has incomplete information about the goodness of patch and there is the possibility that it is better than it appears at present, it is worth continuing for a while on [a reward rate that is less than the average for the environment] in this hope. Under uncertainty one has to take into account what might be, and one is prepared to pay to find out." However, in an environment containing

patches of widely differing quality, there is an optimal price to be paid for gaining such information. In other words, a balance should be struck between staying longer in a poor patch (in order to be sure that it really is a poor patch and not a good patch that is temporarily unproductive) and moving on to another patch which might be better. The optimal sampling time will depend upon a number of factors including the discrepancy between feeding rate in the current patch and the average feeding rate for the environment, and the distribution (poisson, binomial etc.) of food within a patch (Iwasa et al., 1981). S. L. Lima (1984, 1985) has examined the behaviour of downy woodpeckers and starlings foraging in simple stochastic environments. He found good qualitative agreement between the theoretical predictions and the observed sampling behaviour.

Another factor which should influence sampling behaviour is the total amount of time available for foraging. The shorter the time horizon, the less an animal should sample patches to gather information and the sooner it should decide which is the best patch and exploit it (Krebs et al., 1978; Houston et al., 1982). Since no animals have an infinite amount of time available for foraging, then we would expect, in an environment containing a limited number of patches, that they might sample the alternatives and then exploit them in order of profitability.

In the present experiment there were only two patches, one of which - the "hard" patch - was always the same through all trials; the other - the "easy" patch was intended to vary in its profitability. The "hard" patch consisted of a fixed number of hemp seeds stuck into Blu-tak. The "easy" patch consisted of the same number of seeds lightly attached to sticky tape, but only a proportion of them were edible. This proportion was varied between trials and in this way it was hoped to manipulate the profitability of the easy patch so that when edible seeds were abundant there, it was more profitable than the hard patch, and when they were scarce, it became less profitable because of the extra search time required to find the few edible seeds among the inedible majority. (In the event, birds were able to distinguish between edible and inedible seeds, the extra search time was negligible, and the "easy" patch was probably always the more profitable. The implications are discussed in the Results.) The birds' ability to track these changes could be monitored, as could their sampling behaviour.

In addition, the influence of visual cues on foraging decisions could be investigated. Jaeger et al. (1982) found that salamanders foraging for

flies were influenced in their selection by the visual density of flies rather than their actual capture rate. If bullfinches assessed prospective profitabilities of patches by visual appearance, then we would expect the birds to behave similarly in each patch because they looked very similar, both containing the same number of seeds.

Finally, the effects of previous experience were investigated. At the beginning of the experiment, half the birds experienced an easy patch containing no edible seeds, while the easy patch for the remainder contained no inedible seeds. By the end of the experiment all birds were foraging in an easy patch containing edible and inedible seeds in equal quantities.

2. METHOD

2.a. Apparatus

Four adult male bullfinches were kept in outdoor, individual, adjoining aviaries (Fig. 1). While acclimatizing and when experiments were not in progress they were fed from dishes attached to the wire netting walls. Water was always available from a dispenser on the floor. The back wall of each aviary was solid except for two holes permitting entry to the different experimental patches. Access could be denied by raising a flap. Birds could move from one patch to another, only via main aviary. The experimental patches each contained 360 hemp seeds, arranged in three banks of 120 (see plate 3), with a perch underneath each bank. The foraging behaviour of birds 1 and 4 was continuously recorded using a time-lapse video-recorder. Birds 2 and 3 were recorded on ciné-film (Sankyo EM-40 XL). A bird alighting on any perch would trigger a micro-switch causing the cameras to begin filming at the rate of 1 frame every 15 sec. Filming ceased if none of the perches had been occupied for more than 1 minute. The floors of the experimental cages were barred, so that any seeds dropped accidentally or purposely fell through the bars out of reach.

Hemp seeds in the easy patch were lightly stuck onto white sticky tape. In the hard patch, the tape was backed with a layer of Blu-tak, into which the seeds were firmly pressed.

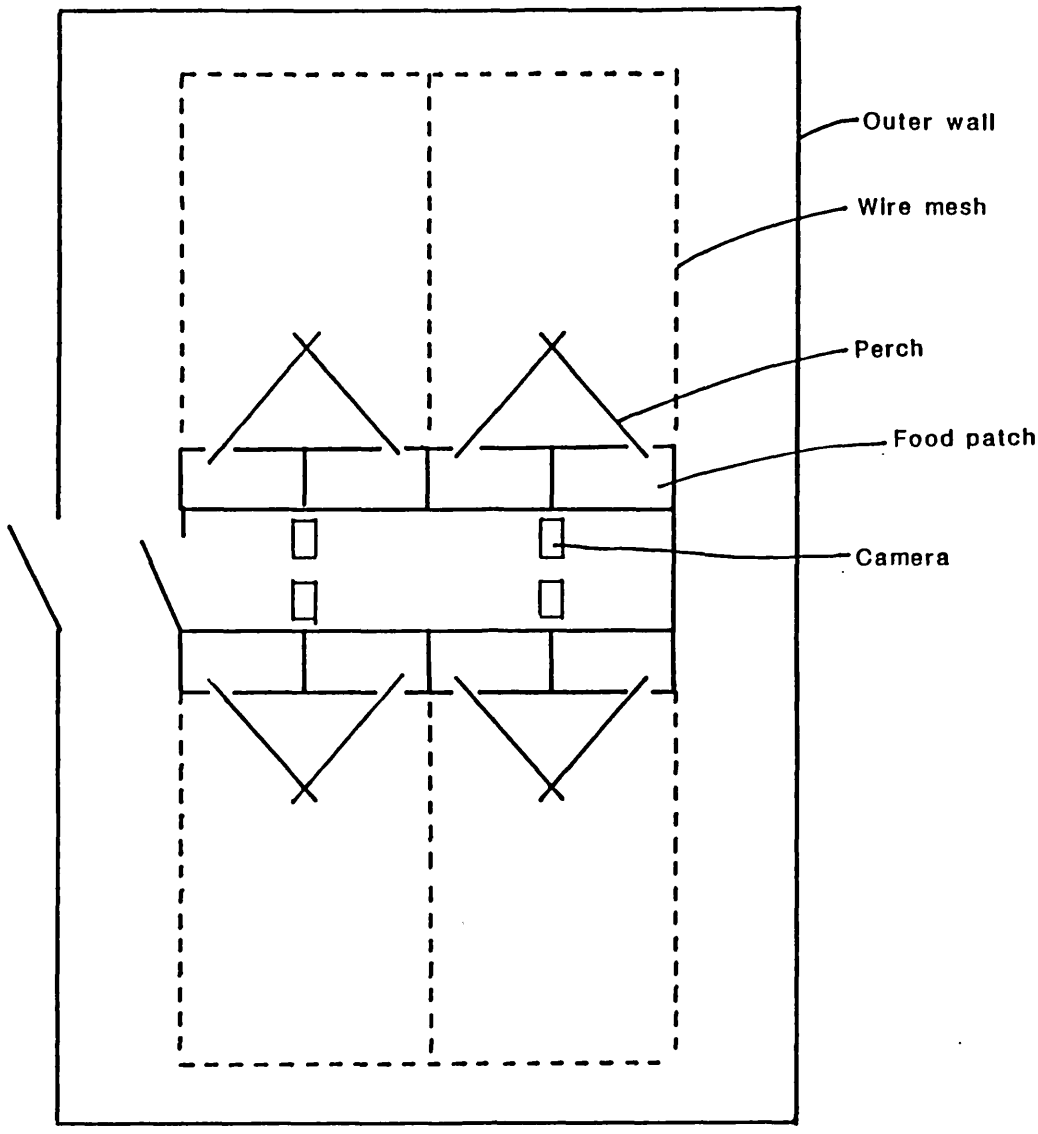
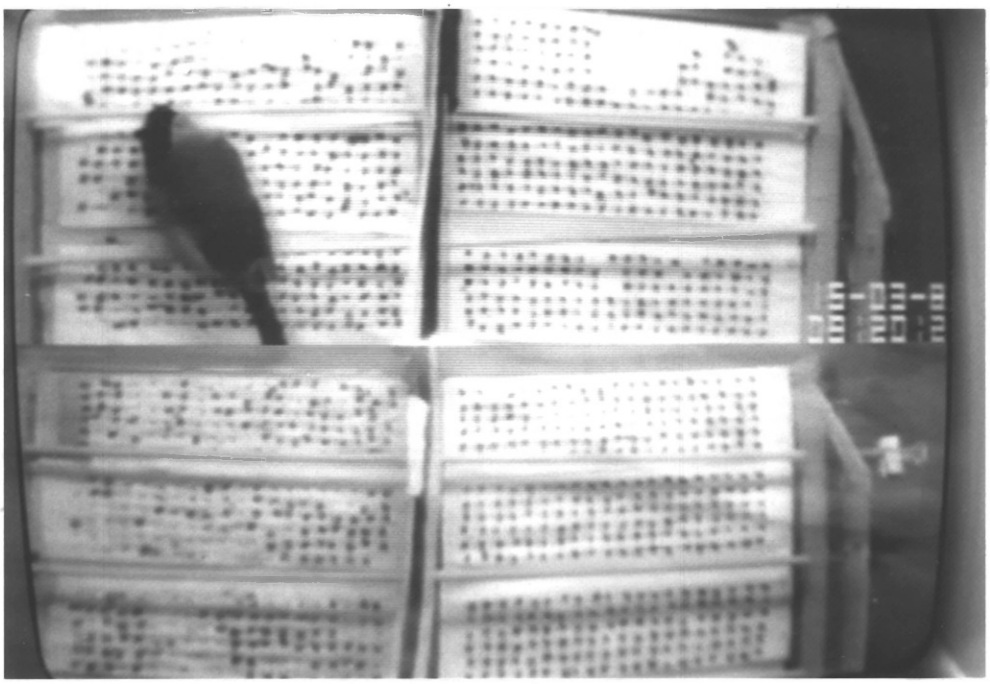


Fig. 1

Plan of the aviaries and experimental cages

Plate 3



Bullfinches feeding in the experimental cages. The "hard" patches are on the left; the "easy" patches on the right.

In several trials the easy patch contained a mixture of edible and inedible seeds. Hemp seeds were made inedible by baking them until they were burned. When birds attempted to handle them, the seeds usually broke into ashes. Because the baked seeds were darker in colour than the raw ones, both types were dyed with a dark wood stain, to make them indistinguishable (at least, to me).

2.b. Procedure.

The hard patch was always the same, containing 360 edible seeds in Blu-tak, for all birds in all trials. The easy patch was changeable. Birds 1 and 2 experienced an easy patch containing 100% edible seeds for the the first three trials. In trials 4,5 and 6 it contained 75% edible seeds, and in the last three trials only 50% of the seeds were edible. Birds 3 and 4, began with an easy patch containing no edible seeds. Conditions improved in the next three trials with 25%, and finally 50% edible seeds in the last three trials. Edible and inedible seeds were randomly distributed in blocks of nine (3x3).

Each trial lasted for two days, during which birds were allowed to feed for 12 hours (6 am - 6 pm), and no food was provided other than that in the experimental patches. There was a gap of one day between trials 3 and 4, and between trials 6 and 7, during which birds fed in the outer aviary.

3. RESULTS AND DISCUSSION

The foraging behaviour of birds 1 and 4 was recorded on videotape and in addition to noting the time spent feeding in a particular patch, it was possible to count the number of seeds remaining at the end of a visit. (The quality of the ciné-films was not good enough to permit this.) However, as the videos were shot on a time-lapse system (at 1 or two frames a second), it was not possible to tell which seeds were successfully dehusked and consumed on a given visit and which seeds were dropped out of reach. Figures 2 and 3 show the cumulative number of seeds removed after successive visits plotted against cumulative foraging time. Figure 2a presents the data for bird 1 during the first three trials when both hard and easy patches contained 360 edible seeds. It may be seen that

Figs. 2 and 3

All figures plot cumulative removal of edible seeds against time. Different symbols represent different trials. Numbers of seeds remaining in a given patch could be counted accurately only when birds were absent from it. Therefore it was not possible to measure seed removal at regular intervals. The points on the graphs generally record the number of seeds remaining after after a bird had left one patch to feed in another.

Fig. 2a. Bird 1, hard patch, trials 1-3 (triangles = 1 circles = 2, squares = 3)
$Y = .060X$ (n=32, s.e.=.002)

Fig. 2b. Bird 1, easy patch, trials 1-3
$Y = .105X$ (n=20, s.e.=.003)

Fig. 2c. Bird 1, easy patch, trials 7-9 (triangles = 7 circles = 8, squares = 9)
$Y = .085X$ (n=25, s.e.=.003)

Fig. 3a. Bird 4, hard patch, trials 1-3 (triangles = 1 circles = 2, squares = 3)
$Y = .040X$ (n=76, s.e.=.001)

($Y = .612X^{.807}$ gave a significantly better fit than a linear regression)

Fig. 3b. Bird 4, easy patch, trials 4-6 (triangles = 4 circles = 5, squares = 6)
$Y = .057X$ (n=7, s.e.=.002)

Fig. 3c. Bird 4, easy patch, trials 7-9 (triangles = 7 circles = 8, squares = 9)
$Y = .074X$ (n=14, s.e.=.003)

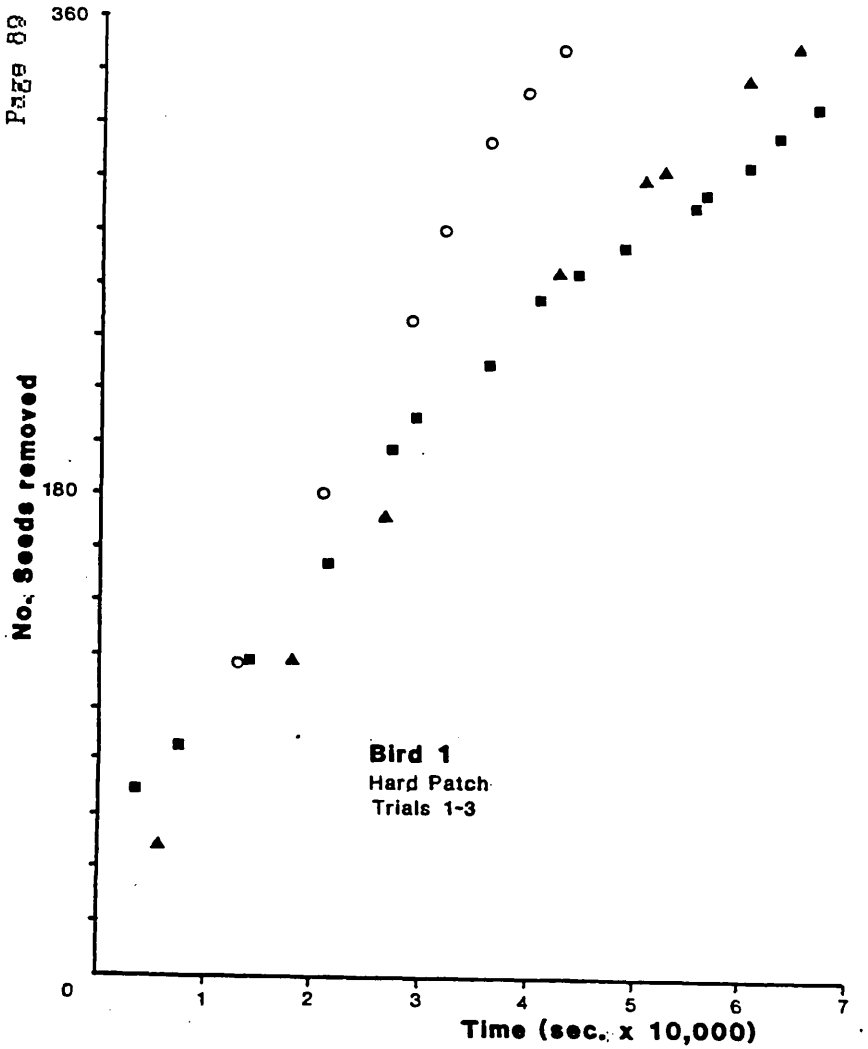


Fig. 2a

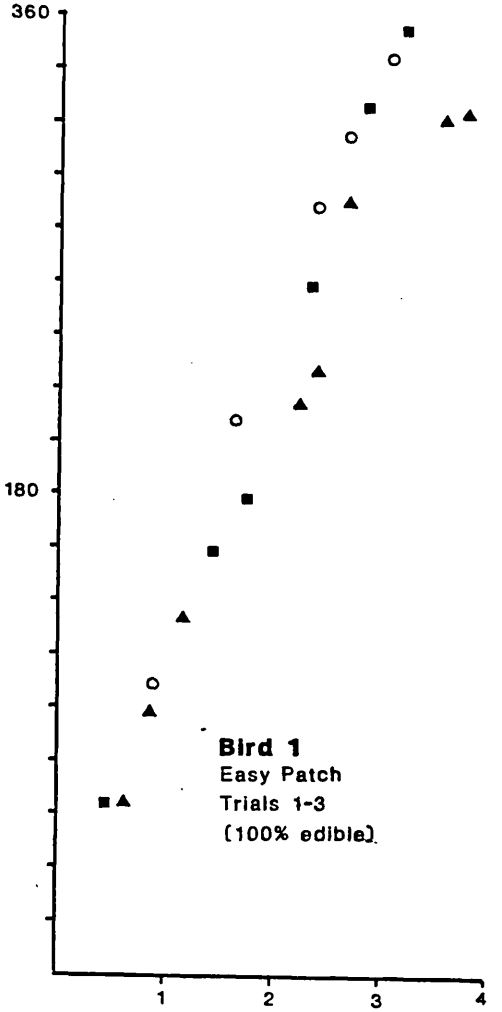


Fig. 2b

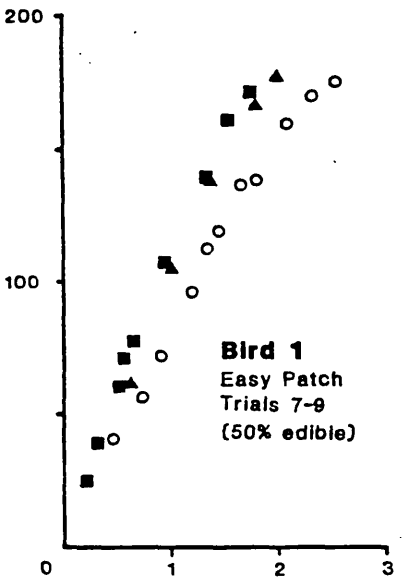


Fig. 2c

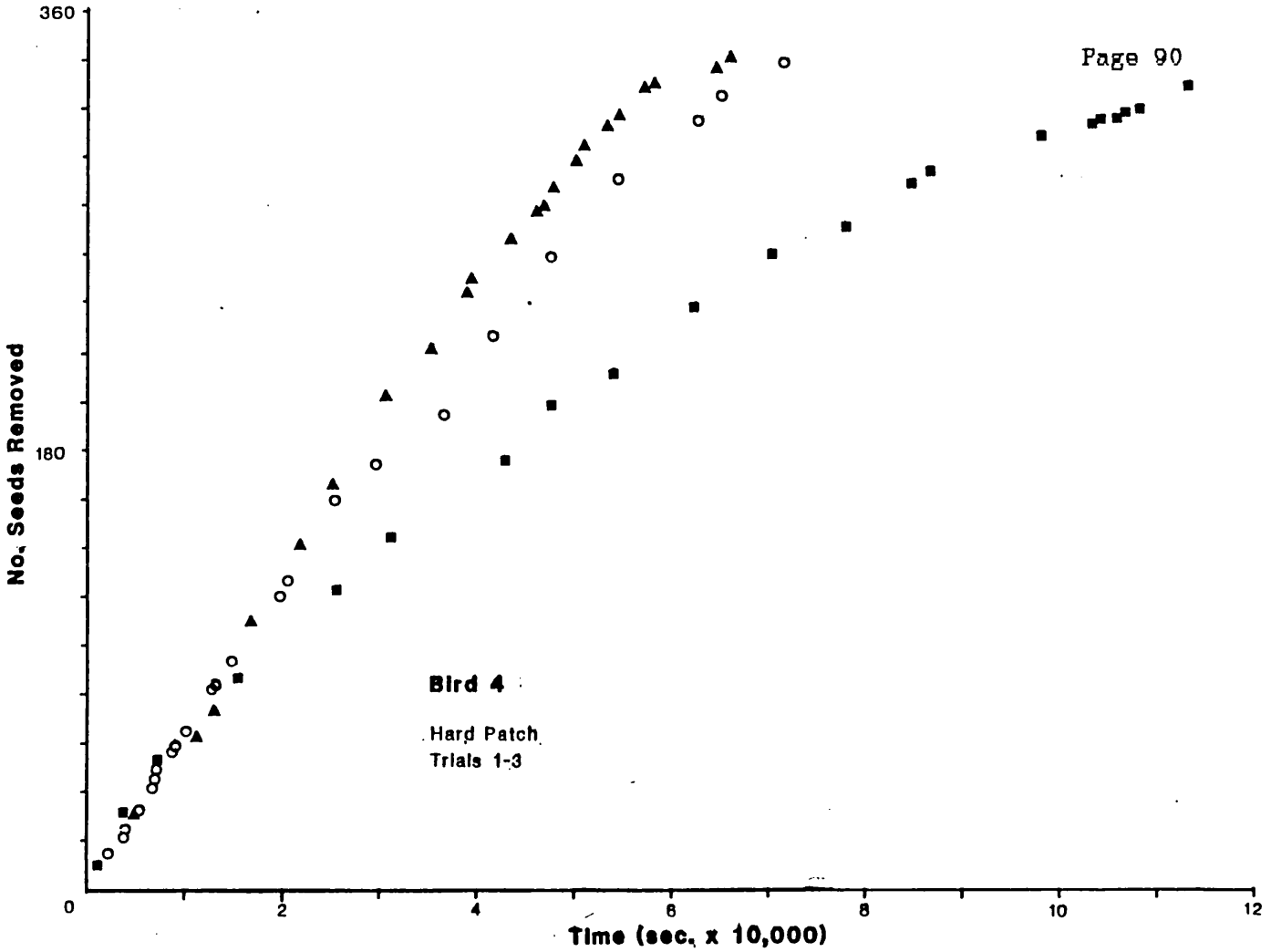


Fig. 3a

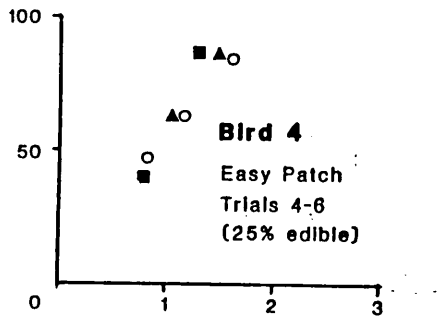


Fig. 3b

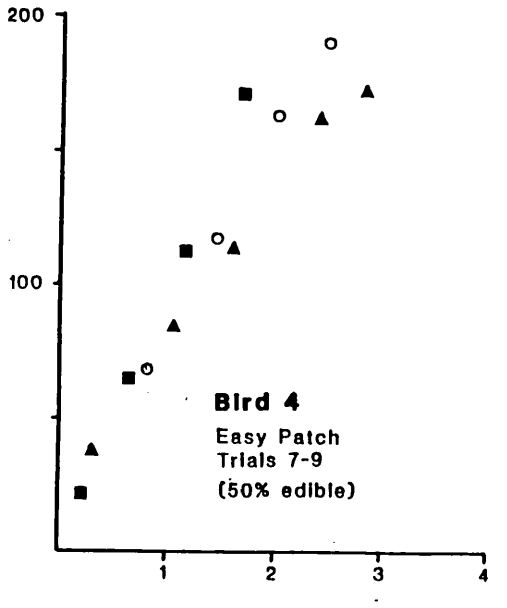


Fig. 3c

the rate of seed removal was higher in the easy patch. (This does not neccesarily mean that the rate of seed *consumption* was also higher. Many more seeds were dropped in the easy patch than in the hard patch, for example (see below). Even disregarding dropped seeds, had the removal rate been identical for both patches, we would not be safe in assuming that they were equally profitable. Seeds in the hard patch, being stuck into Blu-tak, needed more effort to remove than easy seeds. For a given feeding rate, birds would almost certainly have to work harder in the hard patch. This is suggested by the fact that the rate of seed removal in the hard patch becomes slower with time; the more difficult seeds get left till last. This is especially true for bird 4 (Fig. 3a), where a decelerating power function gave a significantly better fit to the data, than did a straight line).

In later trials, when the easy patch contained a mixure of edible and inedible blocks of seeds, it was clear from the video-tapes and ciné-film that all birds could easily distinguish between the two types. They began to remove the inedible seeds only when most of the edible seeds had been eaten. So conspicuous were the different seed types that concentrating solely on the edible seeds incurred little extra cost in search time. This is demonstrated in Figure 2c showing plots of seed removal against time for trials 7-9 when the easy patch contained only 50% (180) edible seeds. It may be seen that bird 1 removed (edible) seeds at a rate that was not significantly slower than in trials 1-3 when the patch was filled with edible seeds. Similarly, bird 4 (Fig. 3b, c) removed edible seeds at a similar rate both in trials 4-6, and 7-9 when the easy patch contained 25% and 50% edible seeds, respectively.

The relatively high, constant rate of (edible) seed removal attained in the easy patch suggests, bearing in mind the earlier qualifications, that it was *potentially* more profitable than the hard patch, even when it was half- or three-quarter-filled with inedible seeds.

3.a. Visit times

3.a.i. Preferences.

Figure 4 shows the proportion of time spent feeding in the hard patch (up until one or other patch was exhausted or until the end of the first day). The hard patch remained constant for all birds in all trials. Unsurprisingly, in trials 1-3 where the easy patch contained only inedible

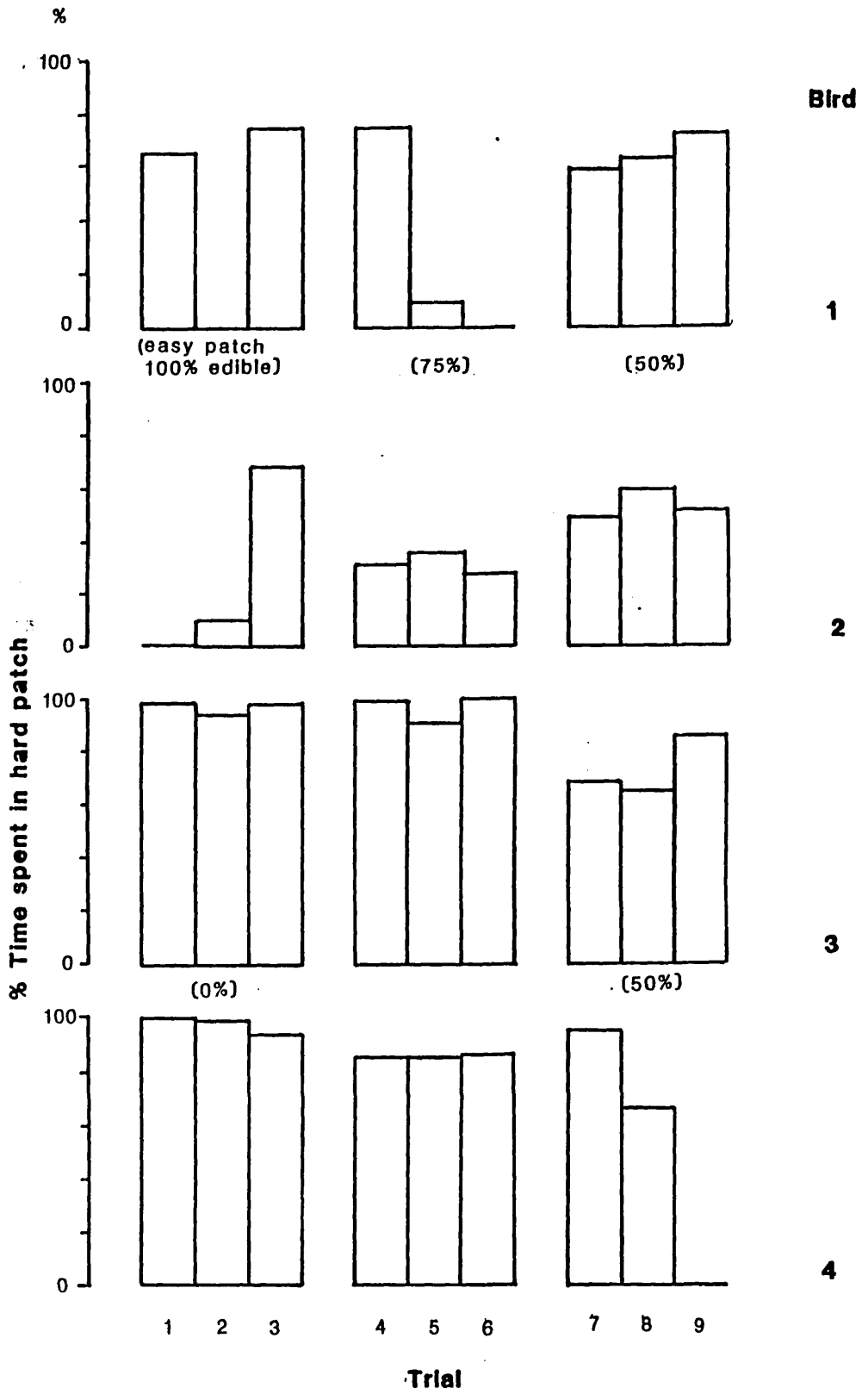


Fig. 4

Proportion of time spent feeding in the "hard" patch.

seeds, birds 3 and 4 spent nearly all of their feeding time in the hard patch. For birds 1 and 2, in the first three trials the seeds in the easy patch were all edible. One might have expected these birds, after some preliminary sampling, to have concentrated on the easy patch, moving on to the hard patch only when the easy patch had become exhausted. Birds 1 and 2 both appeared to adopt this strategy on one of their three trials. However, on half the trials, they spent more than 60% of their feeding time in the hard patch, even though they could probably have done better in the easy patch.

In trials 4-6, the easy patch became richer (an increase from 0 to 25% edible seeds) for birds 3 and 4, and poorer (a decrease from 100 to 75%) for birds 1 and 2, but this appeared to have little effect on their preferences. Bird 4 spent slightly less time in the hard patch, whereas bird 3's behaviour was largely unchanged. The preferences of bird 1 were again unstable: those of bird 2 were more consistent, but neither bird showed a marked change in response to the poorer status of the easy patch. This is perhaps not very surprising because the feeding rate in the easy patch was not greatly reduced by reducing the proportion of edible seeds.

In trials 7-9, all birds were offered easy patches containing equal amounts of edible and inedible seeds. All birds showed clearer changes in preference. Compared with earlier trials, birds 1 and 2 increased the proportion of time they spent in the hard patch, whereas birds 3 and 4 spent less time there. Despite their different histories, birds 1 and 2 did not differ in any obvious way from birds 3 and 4 in the proportion of time they spent in the hard patch. Both groups appeared to track the changing quality of the easy patch and to change their preferences in similar ways. The fact that birds 1 and 2 experienced a deterioration in the easy patch, whereas for birds 3 and 4 it gradually improved, appeared not to influence preference in the final trials, when the easy patch was the same quality for all birds.

Although there were no clear differences between birds in the proportion of time spent in each patch in the final trials, there were other differences in foraging behaviour. Table 1 shows that on the second day of trials 7-9, when food supplies were becoming exhausted, birds varied considerably in the average time spent on a foraging visit. (A visit was defined as the time spent feeding in one patch before switching to the other patch. Where a bird repeatedly left and returned to the

Table 1. Average visit times spent in hard and easy patches on the first and second days of the last three trials (7-9). The easy patch contained 50% edible seeds for all birds.

DAY 1

Hard Patch

	Mean	n	s.e.	F* (p)	t (p)	(1,2 vs.) (3,4)
Bird 1	1495.4	7	454.6			
Bird 2	1166.5	21	211.8	0.97	0.75	(1248.7)
Bird 3	1253.4	9	374.5	(ns)	(ns)	(1660.4)
Bird 4	2067.5	9	750.4			

Easy Patch

Bird 1	709.9	8	266.9			
Bird 2	554.9	21	138.6	0.93	-0.28	(597.6)
Bird 3	531.1	7	99.7	(ns)	(ns)	(576.4)
Bird 4	616.0	8	235.9			

DAY 2

Hard Patch

	Mean	n	s.e	F (p)	t (p)	(1,2 vs.) (3,4)
Bird 1	471.9	20	109.5			
Bird 2	85.3	46	14.5	7.6	2.7	(202.4)
Bird 3	897.6	14	257.5	(p<.001)	(p<.007)	(469.1)
Bird 4	311.2	38	122.7			

Easy Patch

Bird 1	147.1	19	24.0			
Bird 2	80.8	47	13.5	3.1	2.1	(99.9)
Bird 3	296.9	14	89.9	(p<.029)	(p<.034)	(183.4)
Bird 4	139.2	36	56.5			

* F values are for a oneway analysis of variance between all individuals. T values contrast the average visit times of birds 1 and 2, with those of birds 3 and 4.

same patch without visiting the other, then a visit was calculated as the sum of foraging bouts to that patch.) In particular, birds 1 and 2, on a deteriorating regime, paid shorter visits to both patches than did birds 3 and 4, whose food supply was getting better. This result would follow if the decision rule for leaving a patch involves comparing current feeding rate with the feeding rate expected on the basis of past experience. Birds on a deteriorating regime would have higher expectations, and therefore leave sooner, than birds which had previously known only poor conditions.

3.a.ii. Sample-and-exploit *versus* win-stay/lose-shift strategies.

The birds in this experiment visited both patches often enough to learn about the changing quality of the easy patch, relative to hard patch. As the number of edible seeds in the easy patch increased, preference for the hard patch decreased, and, less convincingly, as the easy patch deteriorated, more time was spent in the hard patch. Krebs et al. (1978) and Houston et al. (1982) argue that there are more and less efficient ways of acquiring and acting upon information about food patches and their characteristics. In particular, they suggest that the best strategies should begin by sampling the available food patches and then exploiting the most promising of them. (This is an oversimplification of their argument; the two categories are not mutually exclusive. Since sampling involves eating then it also involves exploiting, and since exploiting provides information about food availability it also involves sampling.) The problem is - how long to sample before exploiting a patch ? (The solution implies that the shorter the time available for foraging, the less time the animal should spend sampling and the more time exploiting). Another possible strategy (one of many) is that an animal stays in any given patch as long as its rate of feeding there is above some threshold rate, and moves on to another patch only when feeding falls below the threshold. This kind of ploy has been called a win-stay/lose-shift (WISLOS) strategy. It is essentially, a "satisficing" (Simon, 1956) strategy in that the animal is not attempting to feed at the highest possible rate, but merely to avoid feeding at a rate which fails to meet its needs. Predictably, a sample-and-exploit strategy outperforms WISLOS in computer simulations (Houston et al., 1982).

The birds in this experiment faced a series of 9 trials, each lasting two days, in which both patches were available for 12 hours a day and supplied nearly all the birds' food. There was an obvious contrast between

the end of one trial (when one or both patches were partially or completely exhausted) and the start of a new trial, when both patches were fully replenished. If birds were employing a sample-and-exploit foraging strategy, then they should have spent less time in the first and second patch visits (when sampling) than on later visits (when exploiting the favoured patch). Figure 5 shows that this was not the case. There was no consistent tendency for residence time within a patch to increase over the first four visits. Only bird 4 demonstrated a reliable pattern and this bird spent *longer* in the first patch it visited than on later visits. Table 2 presents the average time spent on the first visit over all nine trials, compared with the average for all subsequent visits made during the first day (or until one or other patch had been exhausted). Again, it shows that first visits were generally longer, not shorter, than later visits. A similar picture emerges when visit lengths are analysed separately for the hard and easy patches: where differences are significant they indicate that visit lengths became shorter as the day progressed. The data are too few and too variable to draw any firm conclusions, but it is unlikely that birds were employing a sample-and-exploit strategy. A WISLOS strategy comes closer to explaining the data, especially for bird 4, but there are alternative explanations.

For example, Inglis (1983) argues that behaviour is primarily determined by the need to acquire information about the environment, and to build a reliable cognitive model of it. This long-term need may be temporarily overridden by the urge to satisfy more pressing needs such as finding things to eat. A prediction of this theory is that hungry animals should sample or explore less than should sated animals. Each new trial in the experiment reported here, always began early in the morning after a night's deprivation, when, presumably, the birds were at their hungriest. Inglis's "information-primacy" theory would therefore predict that birds should spend longer on the first trial (whilst satisfying their hunger) than on subsequent trials (whilst gathering information).

The data might also be explained within the framework of optimal foraging theory. McArthur and Pianka (1966) and Schoener (1971) have argued that an animal's decision to include poorer items in its diet should be independent of their abundance and should be determined solely by the abundance of the more profitable items: poorer items, regardless of how frequently they are encountered, should be eaten only if this improves the animal's feeding rate. For a foraging animal, a reasonable estimate of the

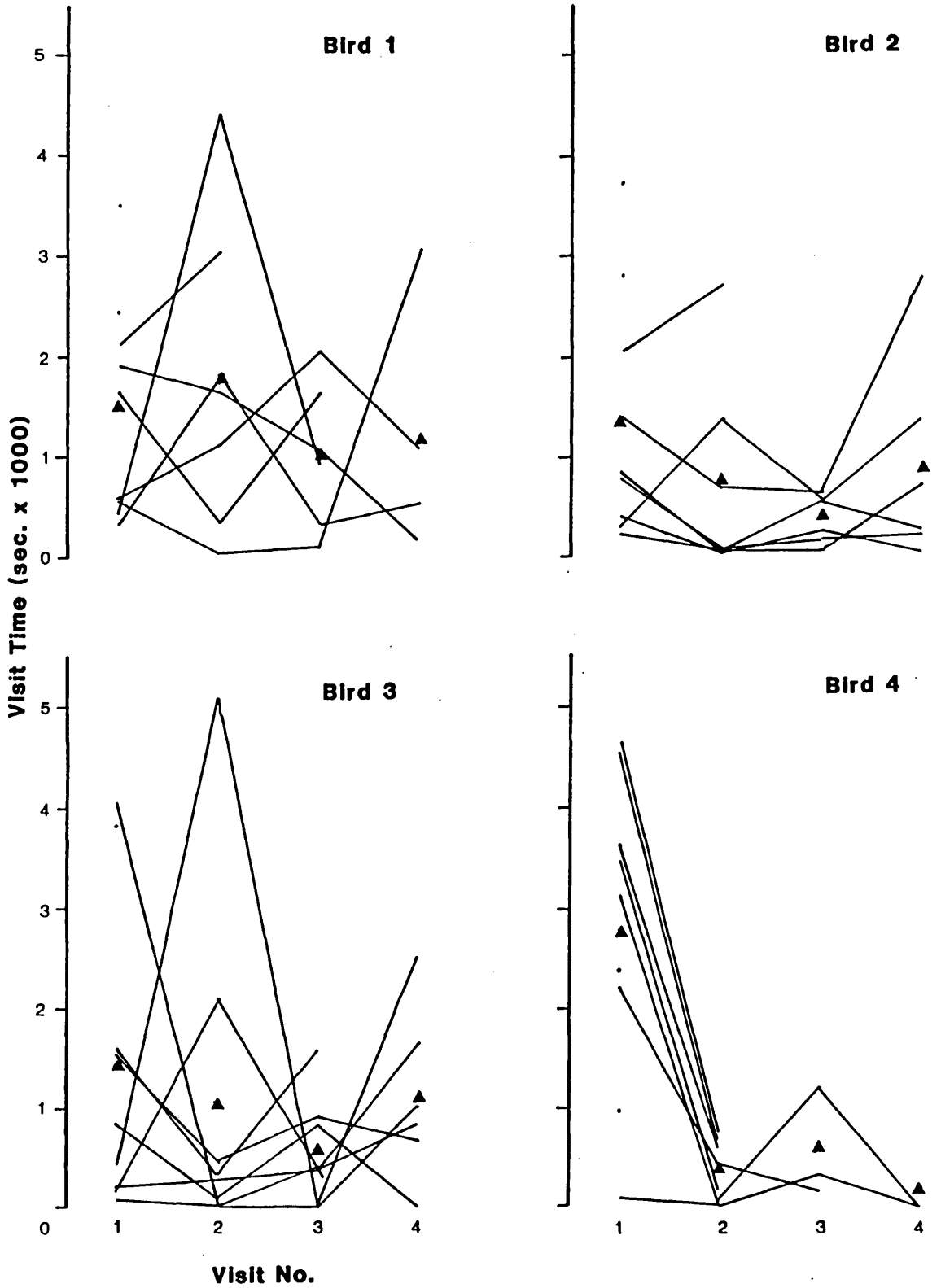


Fig. 5

Length of time spent on successive patch visits during each trial. Triangles represent averages

Table 2. Average duration of first foraging visit of a trial, compared with the average taken over all subsequent visits made on the first day (exlcuding visits made after food had run out of one or other patch)

		Average Visit Times (s)		
		First Visits mean (s.e., n)	Later Visits mean (s.e.,n)	*t* (p)
Bird 1	1st patch vs later patches	1514 (366, 9)	1178 (215, 25)	0.80 (ns)
	1st hard vs later hard	1741 (602, 7)	1382 (301, 8)	0.55 (ns)
	1st easy vs later easy	1549 (348, 9)	590 (157, 10)	2.6 (p<.02)
Bird 2	1st patch vs later patches	1392 (410, 9)	779 (142, 33)	1.77 (ns)
	1st hard vs later hard	540 (265, 7)	988 (288, 11)	-1.1 (ns)
	1st easy vs later easy	1560 (425, 9)	638 (159, 15)	2.4 (p<.05)
Bird 3	1st patch vs later patches	1421 (509, 9)	1018 (230, 32)	0.79 (ns)
	1st hard vs later hard	2151 (597, 9)	1518 (334, 14)	1.00 (ns)
	1st easy vs later easy	230 (60, 8)	294 (115, 10)	-0.45 (ns)
Bird 4	1st patch vs later patches	5558 (1027, 9)	877 (270, 23)	6.14 (p<.001)
	1st hard vs later hard	5558 (1027, 9)	1437 (626, 9)	3.43 (p<.005)
	1st easy vs later easy	738 (235, 7)	296 (164, 7)	1.54 (ns)

abundance of food items in the environment might based on the animal's hunger level (Charnov, 1976). In other words, as preferred prey become scarce, feeding rate falls, and hunger increases. A hungry animal might assume that food is scarce and therefore be content to feed in the first patch it encounters, regardless of its quality. Houston and McNamara (1985) develop another functional model (based on the need to build up energy reserves to survive the night) showing that it can be optimal for very hungry animals to eat all items they encounter, rather than to search for more profitable prey.

Another possibility is that the birds' seemingly sub-optimal performances are an artefact of the experimental design. Birds were allowed to forage in the patches for two days, which was plenty of time to remove all the available seeds. If individuals learned to appreciate this, they may also have learned that no ultimate benefit could be got from maximising food intake in the short-term. Where conditions are more uncertain it may be mistaken to forego short-term benefits. In any case, the following section suggests that birds did not take full account of the fact that the available food had to last them two days.

3.b. Dropped seeds

3.b.i. Differences in diet selection between patches.

All birds, in every trial, dropped more seeds (expressed as a proportion of total number of edible seeds available) in the easy patch, than in the hard patch (Fig. 6). This is the clearest indication we have that the birds were tailoring their feeding behaviour to fit the different patch qualities. The most obvious explanation is that seeds in the easy patch being more lightly attached were more likely to be brushed off accidentally. Videotapes showed that this hardly ever happened. A more likely explanation is that birds were being more selective, rejecting a greater proportion of less-profitable seeds, in the easy patch than in the hard patch. If birds were indeed being more selective in the easy patch then we might expect the seeds they dropped there to differ in some way from the seeds dropped in the hard patch. A crude measure of profitability is given by (seed weight)/(handling time), where handling time is the time required to remove the husk and eat the kernel. For a fixed handling time, small hemp seeds will be less profitable than large ones. However, since handling times were not measured we do not know how they relate to seed weight. We don't know, for example, whether large seeds take a disproportionately longer time to handle and are therefore less profitable than small seeds. Nevertheless, although we cannot predict whether seeds dropped in the easy patch will be heavier or lighter than those dropped in the hard patch, any consistent difference in weight will count as evidence that birds were differing in selectivity between patches. (On the other hand, if no weight differences were found, this would not be compelling evidence against a difference in selectivity).

Table 3 (and Fig. 7) shows that, in the early trials, there were no significant weight differences between seeds dropped in the hard and easy patches. By trials 7-9 however, three out of four birds dropped seeds which were significantly lighter in the hard patch than the easy patch.

The evidence presented in Table 3 suggests, at least in the later trials, that birds were being more selective when feeding in the easy patch. In the easy patch, they dropped many more lightweight seeds which, in the hard patch, they would probably have successfully handled and consumed.

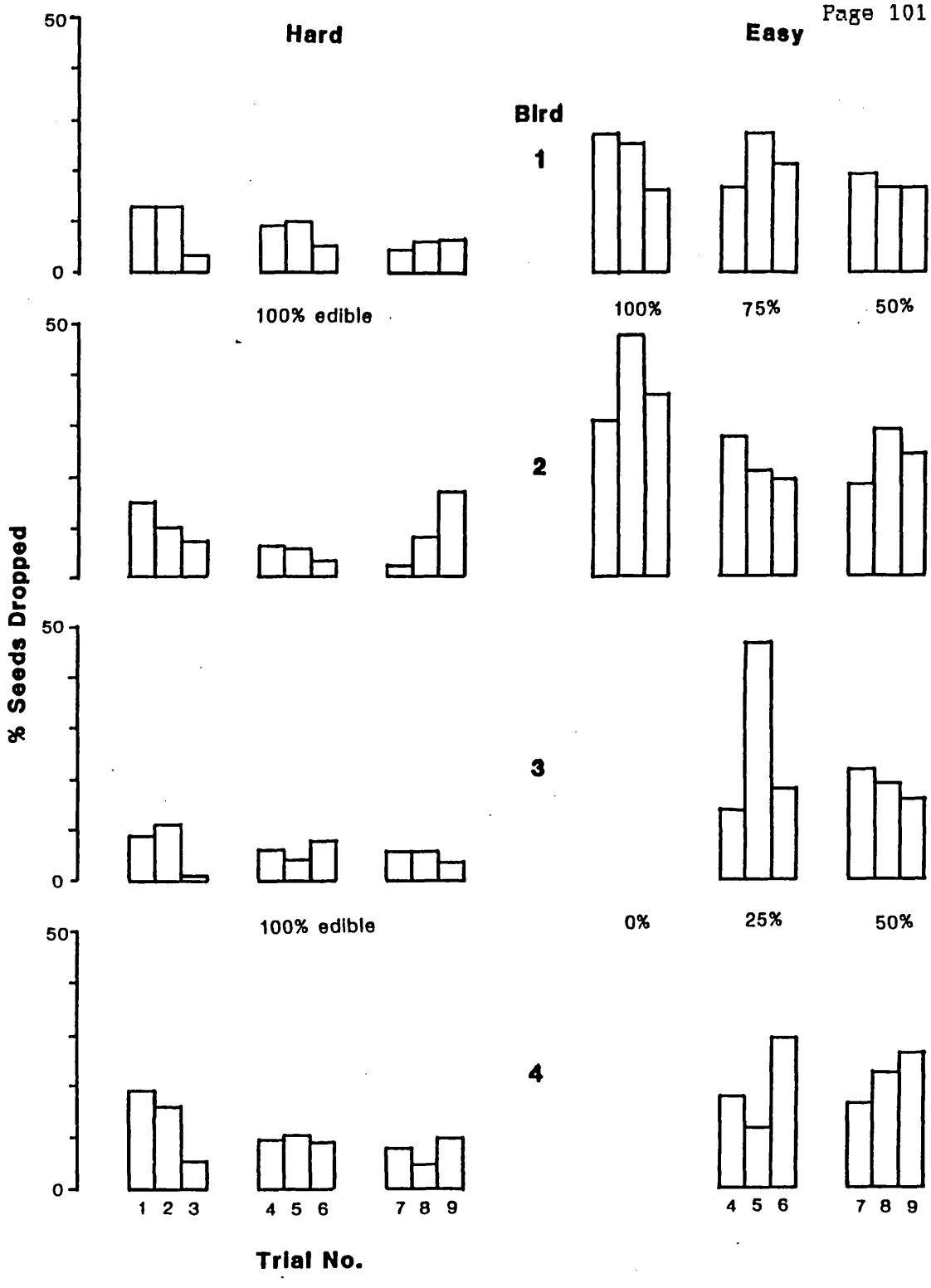


Fig. 6

Number of seeds dropped in hard and easy patches expressed as a percentage of total No. of edible seeds.

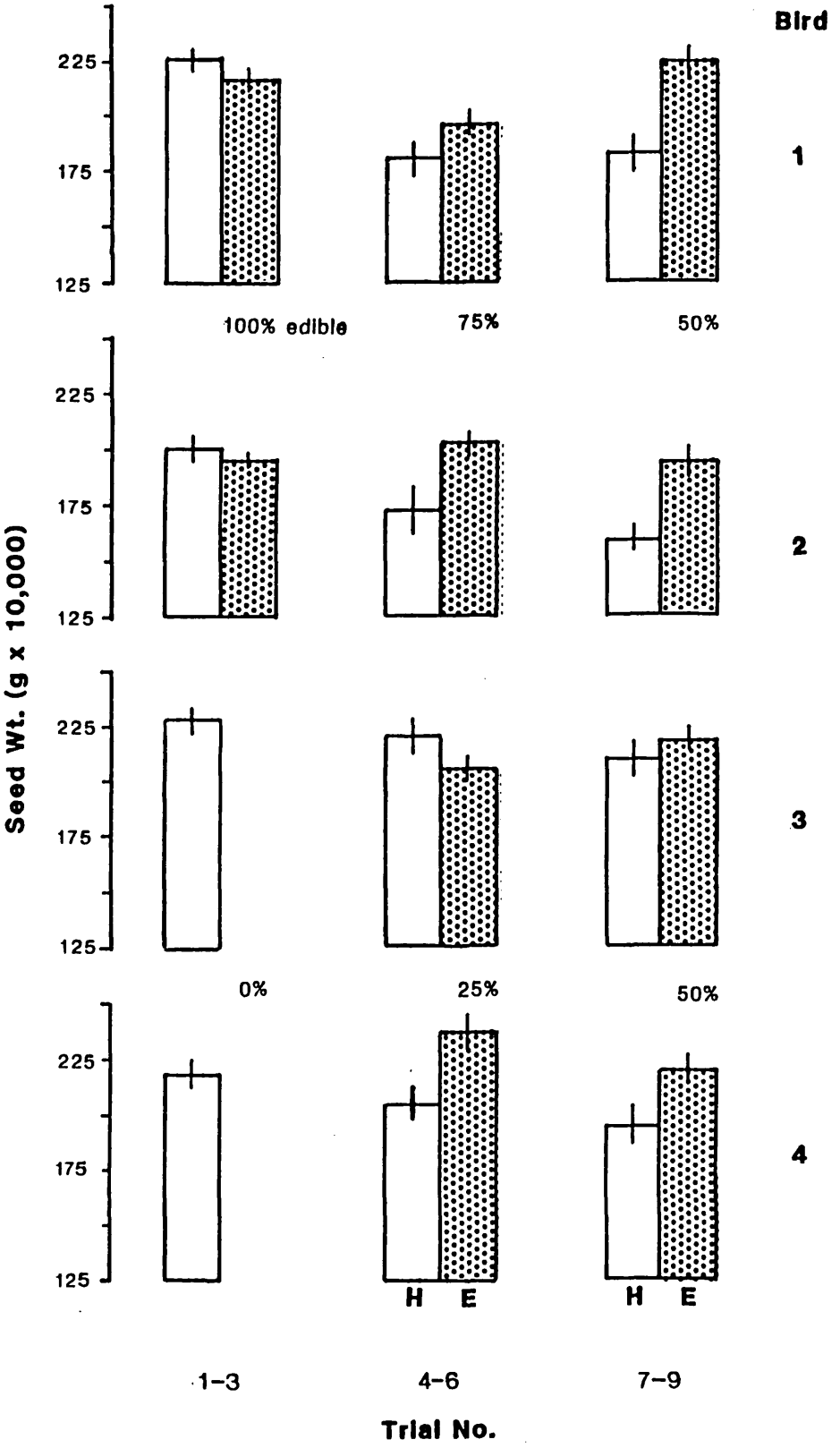


Fig. 7

Mean weight of hemp seeds dropped in hard patches (open bars) and easy patches (shaded bars).

Table 3. Average weights of hemp seeds dropped in easy and hard patches

			mean	s.e.	n	T (p)
Bird 1	Trials 1-3	Hard	226.0	5.5	102	1.27
		Easy	216.6	4.2	241	(ns)
	Trials 4-6	Hard	181.1	8.0	82	-1.64
		Easy	196.9	5.5	165	(ns)
	Trials 7-9	Hard	183.7	9.2	55	-3.6
		Easy	224.5	6.8	87	(p<.001)
Bird 2	Trials 1-3	Hard	200.4	6.7	115	0.62
		Easy	195.7	3.5	390	(ns)
	Trials 4-6	Hard	172.5	10.6	57	-2.72
		Easy	204.6	5.7	178	(p=.007)
	Trials 7-9	Hard	159.8	6.2	94	-3.84
		Easy	194.2	6.2	128	(p<.001)
Bird 3	Trials 1-3	Hard	228.3	6.3	72	
		Easy	-----	---	--	
	Trials 4-6	Hard	220.1	8.8	62	0.86
		Easy	210.5	7.1	70	(ns)
	Trials 7-9	Hard	209.6	7.1	52	-0.89
		Easy	218.7	6.5	94	(ns)
Bird 4	Trials 1-3	Hard	217.8	5.3	139	
		Easy	-----	---	---	
	Trials 4-6	Hard	200.1	7.6	99	-2.98
		Easy	237.0	8.9	52	(p=.003)
	Trials 7-9	Hard	194.1	8.9	76	-2.44
		Easy	219.6	6.2	115	(p=.016)

This result is what one would expect of an animal attempting to maximise its feeding rate in the short term. We have already noted that an animal's decision to include poorer items in its diet should depend on the absolute abundance of the richer items. Where rich items are abundant, animals should be more selective. The hemp seeds used in both patches belonged to the same parent population, and it can be assumed that the mean and variance in seed weight was the same for both samples. The only difference between populations was the extra handling time (and/or effort) required to remove seeds from Blu-tak in the hard patch. If we assume that

this is a constant factor, then a ranking of seed types based on seed weight will not change between patches. The favourite seed size in the easy patch, should also be the favourite in the hard patch. However, if abundance is equated with the rate at which seeds are removed and handled, then preferred seeds will have been more abundant in the easy patch and birds should (and were) less ready to accept less-profitable seeds.

Take, for eaxample, a bird feeding in the hard patch. Having invested some time wresting a poor seed from the Blu-tak a bird must decide whether to dehusk and eat it, or drop it, hopeful that the next seed will be a better one. If the time required to remove the next seed is long relative to the husking time, then the option of rejecting the current seed is relatively unattractive; feeding rate is maximised by holding on to the poor seed and dehusking it. The shorter the removal time, the more often birds should reject poorer seeds and search for better ones. As removal time was shorter in the easy patch, so birds should have been more selective when feeding there.

It is interesting that the birds appeared to ignore visual cues in assessing abundance. Had they relied solely on the evidence of their eyes, they may have behaved rather differently. Both patches always contained 360 seeds, so that an animal relying on a purely visual assessment might have concluded that food abundance was identical and therefore have made the same selection in each patch. Alternatively, if birds were able to judge by eye, the proportion of edible seeds in among the inedible seeds, then birds should generally have been more selective when feeding in the hard patch, since the all the seeds in this patch were edible.

In contrast, Jaeger et al. (1982) found that salamanders feeding decisions could be influenced by manipulating the apparent visual density of flies, while keeping the actual capture rate constant. The authors argue that capture rate is the more reliable measure of abundance, since only by capturing and eating one's prey is it possible to assess handling time and energy value, and hence, profitability. They explain salamanders' susceptibility to visual cues by noting that capture and handling costs are very small for these animals - a tongueflick and swallow with no chewing. Estimates of abundance based on visual assesssments are likely to be similar to those based on capture rates. This was not the case for bullfinches in this experiment, where removal/handling times were longer in the hard patch.

3.b.ii. Effects of experience on diet selection.

Table 4 (and Figure 7) shows the average weight of seeds dropped in trials 7-9 when conditions were the same for all birds. For birds 1 and 2, however, the easy patch had previously been richer, whereas birds 3 and 4 had previously experienced poorer conditions. In the hard patch, seeds dropped by birds 1 and 2 were significantly lighter than those dropped by birds 3 and 4. (There were no significant differences between groups in the easy patch.) It could be argued therefore, that those birds for whom food was getting scarce were becoming less ready to reject poor seeds, whereas birds who found conditions improved were becoming more selective.

Table 4. Comparison of seed weights dropped by individual birds in the final three trials.

	mean	n	s.e.	F* (p)	T (p)	(mean 1,2) (mean 3,4)
Hard Patch						
Bird 1 (↓)	183.7	55	9.2	7.5	3.71	(168.6)
Bird 2 (↓)	159.8	94	6.1	(p<.001)	(p<.001)	(200.4)
Bird 3 (↑)	209.6	52	7.1			
Bird 4 (↑)	194.1	76	8.9			
Easy Patch (50% edible)						
Bird 1	224.4	87	6.8	4.9	1.5	(206.4)
Bird 2	194.2	128	6.2	(p=.002)	(ns)	(219.2)
Bird 3	218.7	94	6.5			
Bird 4	219.6	115	6.2			

Table 5 (and Figure 8) shows average weights of seeds dropped in each patch, in each trial, for each bird. For three out of four birds, there was a significant trend for the weight of seeds dropped in the hard patch to decrease with increasing experience. In other words, three out of four birds became more ready to eat poorer seeds in the hard patch. This suggests that birds were beginning to adapt to the experimental environment in which food supplies were fixed and renewed only after two days. The adaptation was only partial. Feeding behaviour in the easy patch remained consistent throughout the trials, and seeds continued to be dropped in both patches. Furthermore, the tendency to accept smaller seeds was strongest for birds 1 and 2 for whom food was becoming scarcer.

Table 5. Average weight of seeds dropped according to bird, patch, and trial.

		Hard Patch				Easy Patch			
	Trial No.	mean	s.e	n	F(betw. grps) F(linear term)	mean	s.e	n	F(betw. grps) F(linear term)
Bird 1	1	237.3	6.8	44		225.9	6.4	96	
	2	217.1	8.7	47	5.1	219.1	6.0	89	2.7
	3	218.6	20.6	11	(p<.001)	196.5	10.6	56	(p=.006)
	4	172.0	14.3	32		191.6	12.0	44	
	5	174.0	12.4	33	20.3	192.4	8.0	70	0.3
	6	211.9	11.8	17	(p<.001)	207.6	9.3	51	(ns)
	7	215.4	14.9	16		224.2	11.2	33	
	8	168.0	14.9	20		226.7	9.9	29	
	9	173.5	16.4	19		222.2	14.9	25	
Bird 2	1	223.9	9.0	54		219.0	6.3	97	
	2	197.7	12.8	36	6.3	183.2	5.4	165	3.8
	3	153.3	10.9	25	(p<.001)	194.1	6.5	128	(p<.001)
	4	139.7	13.7	23		218.1	8.0	74	
	5	192.1	18.6	21	22.1	185.1	10.9	55	0.5
	6	199.0	21.9	13	(p<.001)	206.0	11.3	49	(ns)
	7	190.4	29.0	8		215.9	11.2	33	
	8	151.1	13.4	27		179.1	10.6	52	
	9	159.6	6.6	59		195.7	9.5	43	
Bird 3	1	220.9	8.9	31					
	2	238.5	8.6	38	1.6				0.9
	3	174.7	42.8	3	(ns)				(ns)
	4	213.7	13.1	21		190.3	15.0	12	
	5	213.0	15.0	16	0.08	212.5	9.3	42	2.3
	6	229.9	16.4	25	(ns)	220.2	15.2	16	(ns)
	7	222.6	11.3	18		213.8	9.7	35	
	8	216.7	11.7	20		211.4	12.8	32	
	9	182.8	12.7	14		233.7	11.0	27	
Bird 4	1	230.0	6.7	65					
	2	203.5	9.1	55	2.5				2.2
	3	217.7	15.7	19	(p=.02)				(p=.05)
	4	178.0	12.6	33		218.3	16.1	16	
	5	200.5	13.0	34	4.25	217.9	23.9	10	0.005
	6	222.5	12.9	32	(p=.04)	255.1	10.9	26	(ns)
	7	186.4	13.4	26		199.1	12.4	28	
	8	180.5	21.8	17		220.2	11.3	40	
	9	207.1	13.6	33		231.4	8.7	47	

The upper F value in each case is for a one-way analysis of variance between trials. The lower value tests the hypothesis that there is a linear trend across trials.

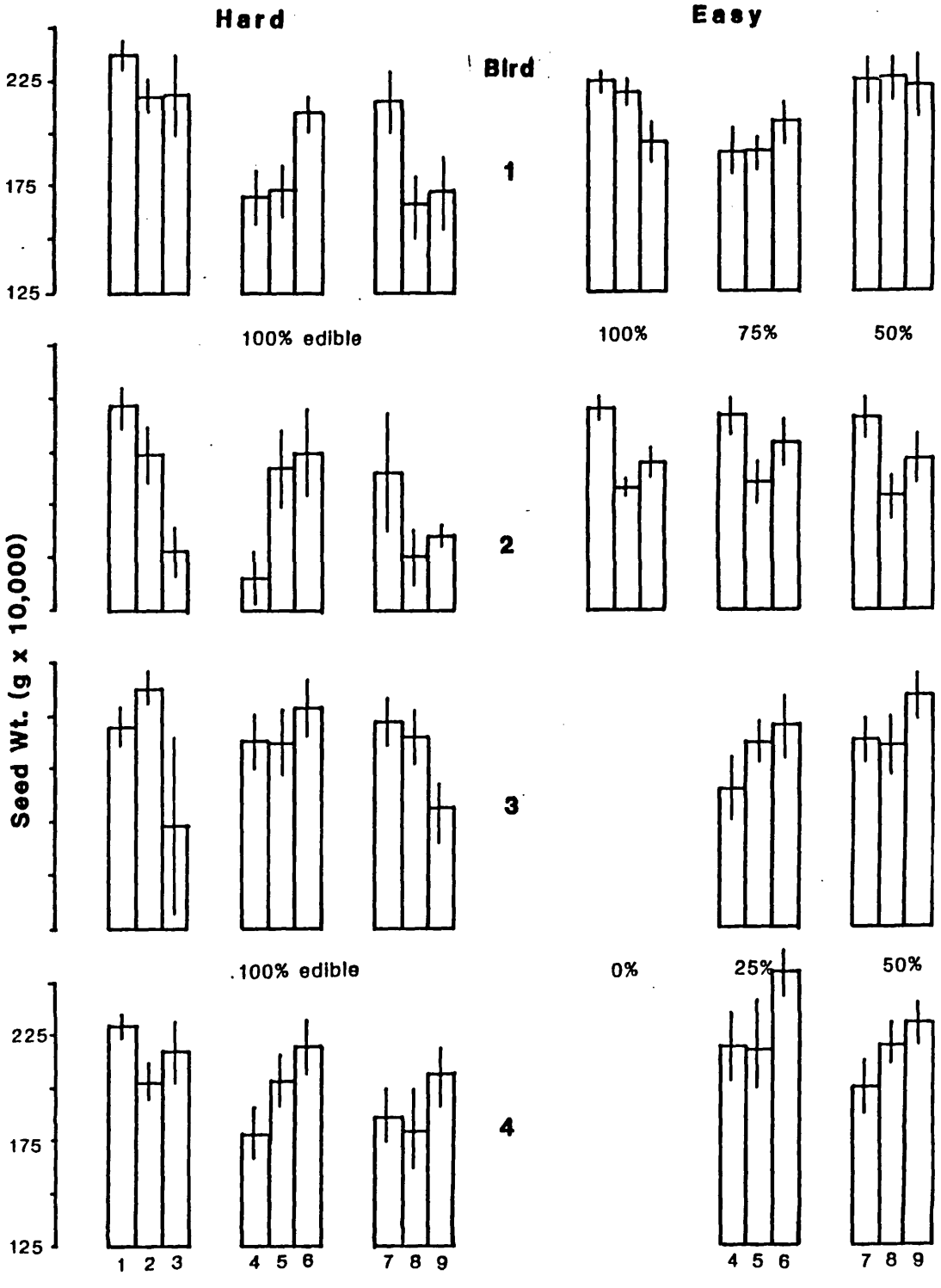


Fig. 8

Mean weight of hemp seeds dropped in hard and easy shown separately for each trial.

4. CONCLUSION

The easy patch was probably more profitable than the hard one, even when only a quarter of the seeds it contained were edible. Birds 1 and 2 should have preferred the easy patch in all trials, and birds 3 and 4 in all except the first three trials. In fact, as the number of edible seeds decreased, birds 1 and 2 gradually spent less time in the easy patch even though it continued to be more profitable. Birds 3 and 4 only gradually came to spend more time there, as the number of edible seeds increased. The large number of edible seeds in the hard patch appeared to be attractive, despite their being difficult to remove.

In the final three trials, when conditions were the same for all birds, preferences (as measured by residence time in a patch) seemed to be little influenced by the birds' prior histories. However, birds 1 and 2, on a deteriorating regime, switched more often between patches than did birds 3 and 4 for whom conditions were improving.

The pattern of visits at the beginning of each new trial did not follow a "sample-and-exploit" strategy. The first visit to a patch tended to be longer than subsequent visits.

Birds dropped many more seeds in the easy patch than in the hard patch, where dropped seeds were likely to be lighter in weight. They were behaving in accordance with optimal foraging theory which predicts that animals should be more discriminating when preferred foods are plentiful and less discriminating when food density is scarce. Birds appeared to rely on the rate at which seeds could be removed as a measure of their abundance, rather than by visually assessing their numbers.

As the sequence of trials progressed, birds generally became less ready to reject small seeds when feeding in the hard patch. This suggests they were beginning to appreciate that the supply of seeds in a trial was fixed. On the other hand, birds continued to drop many seeds suggesting that they were still trying to achieve a high feeding rate in the short term. Previous history appeared to have some influence in that birds on a deteriorating regime were more ready to accept small seeds than birds on an improving regime, in the same circumstances.

Chapter 4

A causal model of risk sensitivity

1. INTRODUCTION

1.a. Risk sensitivity.

In several recent papers, it has been argued that foraging animals should compare not only how much food is available from alternative sources, but also how variable is the food supply (Caraco, 1980; Stephens, 1981; Stephens and Charnov, 1982; McNamara and Houston, 1982; Krebs, Stephens and Sutherland, 1983). These authors have predicted the circumstances under which an animal should prefer a variable food reward to a constant reward of the same average value. McNamara and Houston (1982) provide a detailed explanation: the argument may be stated more simply as follows.

Suppose an animal has the choice of feeding at one of two food stations. Both stations offer the same mean rate of food intake, but one station delivers a fixed food reward in a fixed time, while the other delivers a randomly varying meal size (sometimes more, sometimes less than the fixed reward). When the mean rate of food intake in both stations would lead the animal to fall short of some critical need (e.g. the amount of food at the end of the day needed for an animal to survive the night) then feeding at the fixed station results in certain death, whereas feeding at the variable station may possibly result in survival; by chance, the animal may obtain enough large rewards to satisfy its energy budget. Conversely, when the food stations offer average exploitation rates above the minimum requirement then the fixed station offers guaranteed survival, whereas feeding at the variable station is to risk death. The argument has been summarised in the form of the expected energy budget rule (EEB), namely, "Be risk averse, if your expected energy budget is positive; be risk prone if your expected energy budget is negative," (Krebs, Stephens and Sutherland, 1983).

Until recently (before 1985), the crucial empirical support for this prediction has come from studies by Caraco, Martindale and Whittam (1980) using yellow-eyed juncos (*Junco phaenotus*), Caraco (1981) using dark-eyed

juncos (*Junco hyemalis*) and Caraco (1983) using white-crowned sparrows (*Zonotrichia leucophrys*). These papers claim to be empirical demonstrations of risk sensitive foraging preferences, confirming the predictions of the EEB rule.

In each of these papers the same basic method was followed. Typically, birds, in a series of trials, were confronted with a choice between feeding at a station offering a fixed reward (e.g. 4 seeds) or choosing a station where the reward was variable (2 or 6 seeds presented with probability 0.5). However, the delay between successive trials was engineered to be proportional to the number of seeds eaten on the preceding trial. Thus at the food station that always provided 4 seeds, the subsequent interval before the next trial was always 4 mins; and at the variable station a reward of 2 seeds was followed by a 2 minute delay and 6 seeds by a 6 minute delay. (Presumably this was done to ensure that hunger levels at the start of each trial were independent of the food received on the preceding trial, and so making it less likely that the station chosen on one trial was influenced by the result of the preceding trial.) Regardless, therefore, of the choice made, at the beginning of each trial, the birds would have experienced the same rate of food intake (1 seed per min). By the end of any trial, birds choosing the variable station would not have suffered a better or worse than average rate of feeding, and therefore they incurred no greater "risk" than if they chose the constant station. Nevertheless, Caraco et al.'s results showed that birds preferred the variable station when running below budget and the constant station when above budget.

Barnard (personal communication) acknowledges the lack of variance in feeding rate in these experiments but argues that "the prediction regarding which station to visit is based on the probability of the *next* visit guaranteeing survival, not the effect of several visits on intake rate." This may be so, but the birds can only estimate this probability on the basis of their past experience, which in this case is one of a uniform feeding rate, regardless of the patch chosen.

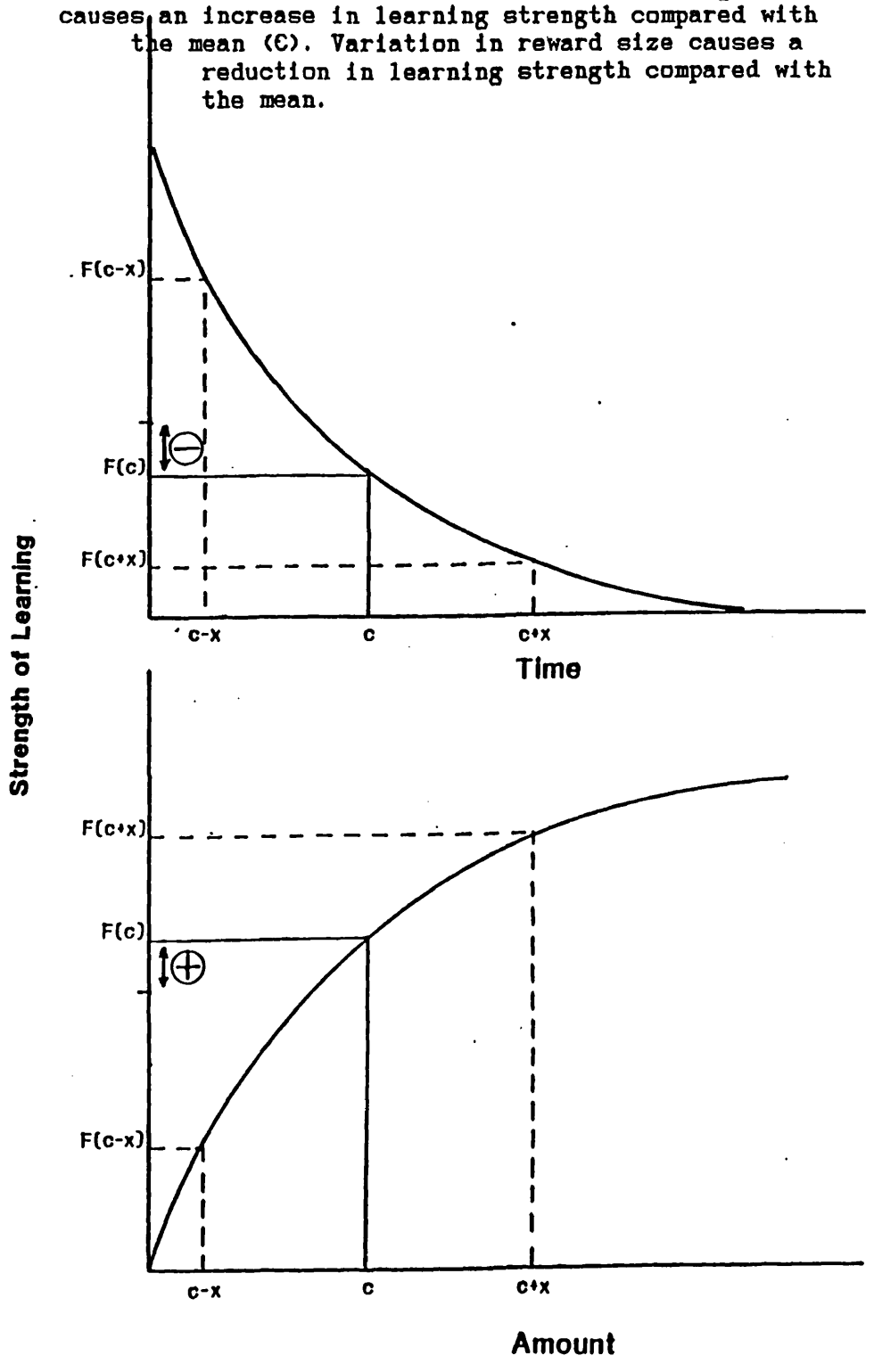
Although they cannot be said to be risk prone or averse in the functional sense proposed by Caraco, we need to explain why his birds changed their feeding preferences in apparent agreement with the EEB rule. Where animals appear to make "mistakes" (as judged by the theoretically optimal behaviour) we may learn something about their perceptions, the cognitive mechanisms underlying their choices (see for example the

psychological studies of optical illusions in humans, (Gregory, 1971)). The behaviour of Caraco's birds may not have been "mistaken", but in the absence of an alternative functional reason, it requires, at least, some causal explanation.

Although Caraco was the first to have manipulated energy budgets in this context, there is an established literature on the preferences of animals for, or their aversions to, variable rewards. It is somewhat contradictory. Krebs et al (1983) note that operant psychologists, manipulating delay between rewards, usually obtain risk proneness, whereas behavioural ecologists, varying the size of rewards, find their animals to be risk averse. That subjects in operant conditioning experiments generally prefer variable interval (VI) rewards to fixed interval (FI) rewards of the same value, is well known, having first been noted in rats by Pubols (1962) and by Logan (1965b). The phenomenon was established in pigeons by Herrnstein (1964), Fantino (1967), Killeen (1968), Davison (1969) and others since. As Pubols (1962) points out, a preference for variability in reward delay is an expected consequence of the relationship between delay of reinforcement and strength of learning. As long ago as 1932, Hull argued, from the behaviour of rats in maze learning experiments, that the effect of a reinforcer on speed of learning decreases with its delay and that the curve relating the two is negatively accelerated. For a convex shaped curve, as this is (Fig. 1a), Jensen's inequality stipulates that the effect of varying the delay of reinforcement should increase its effect, compared with a constant delay of the same average duration.

Behavioural ecologists, lacking the operant psychologists' automated feeding devices, have generally found it easier to manipulate the size of a reward rather than its timing. Real (1981) and Waddington, Allen and Heinrich (1981) found that bumblebees (*Bombus edwardsii*) avoid flowers providing variable amounts of nectar. Among birds, Stephens and Ydenberg (quoted in Krebs et al., 1983) found that great tits (*Parus major*) avoided variation in the number of fly pupae offered, while Wunderle and O'Brien (1985) have demonstrated clear risk aversion in bananaquits (*Coereba flaveola*) feeding on artificial flowers offering different amounts or concentrations of nectar. There seems to be a general tendency for animals to prefer constancy of reward size. This suggests that the value of a reward increases with its size in an asymptotic fashion. Again, earlier work by operant psychologists has suggested such a relationship (e.g., Hull, 1943; Dufort and Kimble, 1956; and Logan, 1965a.) Being concave

Fig. 1
The relationship, postulated by operant psychologists, between strength of learning and a) delay of reward and b) amount of reward. Variation in reward timing (C±x) causes an increase in learning strength compared with the mean (C). Variation in reward size causes a reduction in learning strength compared with the mean.



in shape (Fig. 1b), a variable reward would be less valuable than a constant one of the same average size. An exception to this rule is Leventhal et al. (1959) who found that rats preferred to visit a goal box where reward size varied.

In experiments where risk sensitivity has been examined in relation to energy budget, Barnard and Brown (1985) have confirmed Caraco's findings, showing that shrews (*Sorex araneus*) prefer variable food sources when running below budget, and avoid variability when above budget. On the other hand, Hill, Riopelle and King (1983), using rhesus monkeys (*Macaca mulata*) found that protein-starved animals were more likely than controls to avoid food stations where meal size was variable; in this experiment the delay between trials appears to have been held constant. More recently, Battalio et al. (1985) and Kagel, MacDonald et al. (1986) have explicitly attempted to reproduce Caraco's findings using rats. In these experiments, reward size (food in one case, and water in the other) was varied, while in a deliberate departure from Caraco's procedure, delay between trials was held constant. They found that rats were generally risk averse, even when run below budget. Very recently, Wunderle, Castro and Fetcher (1987) have been unable to show risk proneness in bananaquits feeding on negative energy budgets. When the amount of nectar was varied at a particular type of feeding station, birds always preferred the constant stations.

Possibly, these differing results stem from the different procedures, apparatus and species used. For example, operant psychologists tend to keep their animals at 80% of ad libitum body weight, and very hungry animals may be more likely to take risks. Psychologists also use domesticated rats and pigeons which may have had their tendency to avoid risks bred out of them.

Alternatively, it is possible to devise a unifying causal model which results in animals being risk prone when food arrives at variable times (the operant psychologists' finding); risk averse when food arrives in variable quantities (the behavioural ecologists' finding); and "variance prone" (i.e. no real risk is incurred) if food size and delay are varied proportionately and EEB is negative, and "variance averse" when EEB is positive (Caraco's finding).

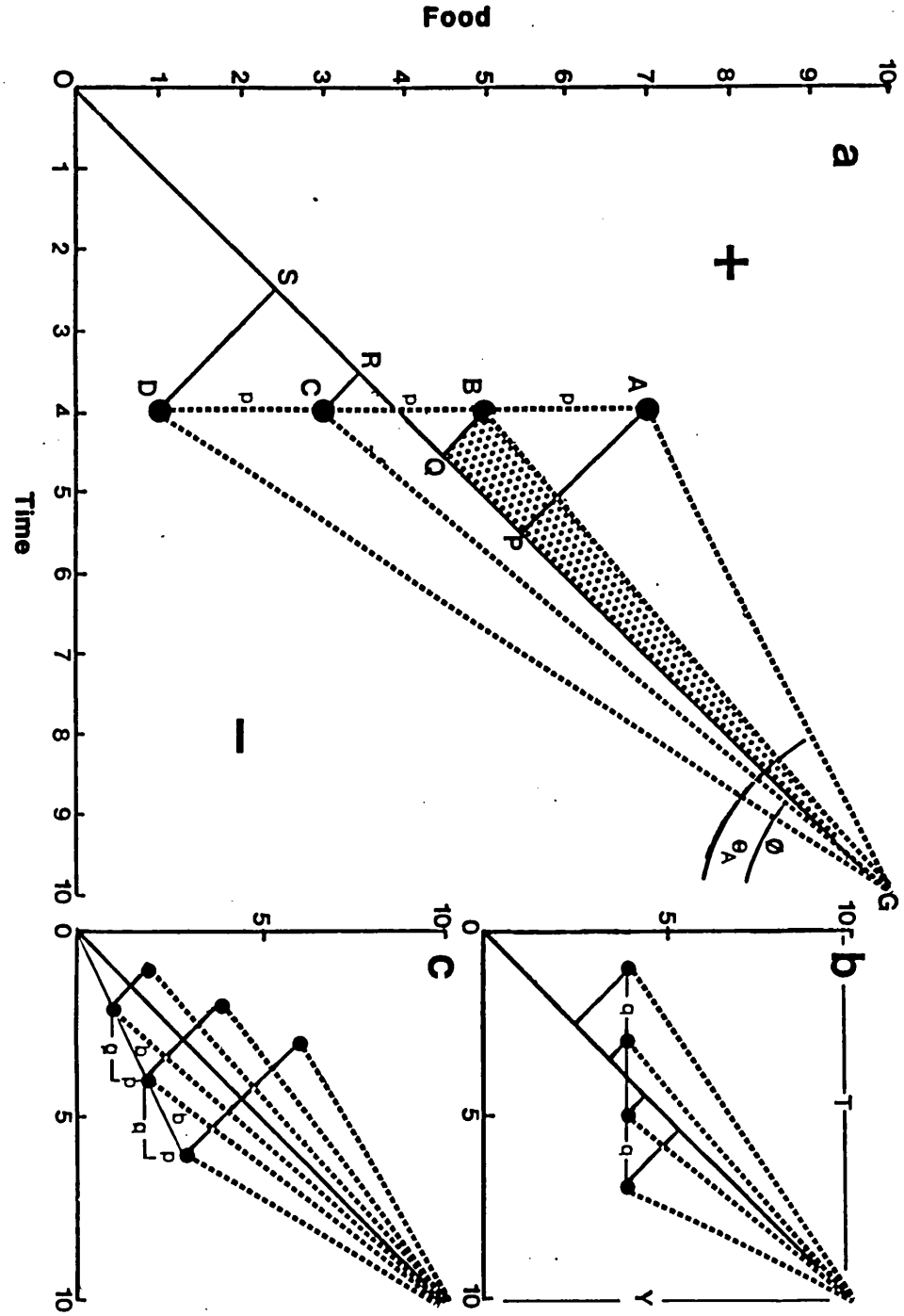
Fig. 2

a) Expected hunger/satisfaction for an animal feeding at a constant station (B) giving 5 food units, compared with a variable station (A or C) giving 3 or 7 units. The animal needs to find 10 food units in 10 time units (G). On average, both stations provide food at greater than the necessary feeding rate. The expected satisfaction from feeding at the constant station is shown by the shaded triangle BGQ.

b) As for 2a) but both constant and variable stations offer a feeding rate that is less, on average, than that required by the energy budget. The expected hunger on feeding at the constant station (C) is shown by the shaded triangle CGR.

c) Expected hunger/satisfaction for an animal feeding at a constant station giving a fixed reward after a fixed delay, compared with a variable station offering the same reward after a variable delay.

d) Expected hunger/satisfaction for an animal feeding at a constant station giving a fixed reward after a fixed delay, compared with a variable station giving a variable reward after a variable delay. Regardless of the station chosen, the feeding rate is always constant.


Food
Time
a
b
c
+
−
S
R
Q
P
A
B
C
D
p
q
G
T
Y

2. A MODEL (version I)

Suppose that a bird needs to balance an energy budget of 10 food units to be consumed in 10 time units (point G in Fig. 2a). Its minimum necessary feeding rate is given by the budget line OG. In the example given in Fig. 2a, the bird has a choice of feeding at a station giving a constant reward of 5 food units in 4 units of time (point B) or choosing to feed at an alternative station equiprobably giving 7 units (point A) or 3 units (point C) in the same 4-unit time period. At both feeding stations, on average, the bird will be feeding at more than the necessary rate (OG); it will have a positive expected energy budget in Caraco's terms. Suppose that a positive deviation (AP) from OG is attractive (call it "satisfaction"), and that negative deviation (CR) is aversive (call it "hunger"), then the minimum amount of satisfaction or hunger the bird can expect to meet after feeding at the various stations and before reaching its goal is given by the areas of triangles AGP, BGQ and CGR. Suppose therefore, that the bird chooses between feeding stations, not according to their mean rate of food delivery, but according to the subsequent amount of "satisfaction" or "hunger" it can expect to endure on the way to its goal ie. according to its instantaneous deviation from the budget line integrated over the time remaining before the budget must be balanced. A bird will choose the variable station if, respecting the sign of deviation from OG,

$$\frac{\Delta AGP \tilde{+} \Delta CGR}{2} > \Delta BGQ$$

The area (H) of any given triangle representing expected hunger/satisfaction is given by the following formula,

$$H = \tfrac{1}{2}[\sin(\theta-\phi).\cos(\theta-\phi)].[(T-t)^2 + (Y-y)^2] \qquad (2.1)$$

where T is the total time available for foraging and t is time passed; and Y is total amount of food to be eaten and y is food already eaten. The angles θ and ϕ are shown in Figure 2a. Using the Sine and Cosine rules, H may re-expressed as,

$$H = \tfrac{1}{2}[(\sin\theta.\cos\phi - \cos\theta.\sin\phi).(\cos\theta.\cos\phi + \sin\theta.\sin\phi)].[(T-t)^2 + (Y-y)^2]$$

$$\sin\theta = \frac{T-t}{[(T-t)^2+(Y-y)^2]^{1/2}} \quad ; \quad \cos\theta = \frac{Y-y}{[(T-t)^2+(Y-y)^2]^{1/2}}$$

$$\sin\phi = \frac{T}{(T^2+Y^2)^{1/2}} \quad ; \quad \cos\phi = \frac{Y}{(T^2+Y^2)^{1/2}}$$

Substituting and rearranging gives,

$$H = \frac{(y.T - t.Y).(Y^2 - y.Y + T^2 - t.T)}{2.(T^2 + Y^2)} \qquad (2,2)$$

When *amount* of food is manipulated at the variable station

The difference in expected hunger (H) for points A,B and C is determined solely by the differing amounts of food received (y). Since points A and C (representing food rewards from the variable station) are equidistant (see Fig. 2a) from point B (the constant station), the amounts can be written as,

$y_A = z + 2p$, $y_B = z + p$, and $y_C = z$

where p is the absolute value of the difference A-B (= B-C) and z is a constant. Substituting these values of y into H, an animal will choose the variable patch if,

$H_B - \frac{1}{2}.(H_A + H_C) < 0$

that is, if

$$\frac{T.Y.p^2}{2.(T^2+Y^2)} < 0 \qquad (2,3)$$

where p^2 is the variance of reward size at the variable station. Since T and Y are always positive then this difference must also be positive. Birds should prefer the constant station in this case, because this station offers greater expected satisfaction. Similarly, when the mean reward offered by the food stations lies below the budget line (point C in Fig. 2a, with points B and D representing the variable station), the difference in expected hunger is again positive, and since the bird is minimising hunger, it should again choose the constant station. *Thus, when size of food reward is the manipulated variable, animals should always choose the constant station, regardless of energy budget.*

When *delay* of food is manipulated at the variable station

When delay is the manipulated variable (Fig. 2b) the difference, in terms of expected satisfaction/hunger, between constant and variable stations is again given by,

$$-\frac{T.Y.q^2}{2.(T^2+Y^2)} \qquad (2,4)$$

where q^2 represents the variance in delay at the variable station. *This difference is always negative, and so the bird should choose the variable station, regardless of energy budget.*

When *amount* and *delay* are manipulated at the variable station

When reward size and delay are manipulated together and proportionately (Fig. 2c) the difference obtained by subtracting the expected hunger of the variable station from that of the constant station is given by,

$$\frac{(T.Y.(p^2-q^2) + p.q.(T^2-Y^2))}{2.(T^2+Y^2)} \qquad (2,5)$$

Given Y > p and T > q, then the above difference is always negative for Y/T > p/q, and is always positive for Y/T < p/q. *Thus the bird should prefer the constant station when running above budget and the variable station when running below.*

The absolute value of the difference in expected hunger between constant and variable stations can be re-expressed more simply (see Appendix 1), as

$$\frac{\sin\alpha.\cos\alpha.(p^2)}{2} \qquad \frac{\sin\alpha.\cos\alpha.(q^2)}{2} \quad \text{and} \quad \frac{\sin\alpha.\cos\alpha.(p^2+q^2)}{2}$$

for experiments where food size, delay, and size and delay, are manipulated, respectively. (The angle α is shown in Fig. 2c.) In general therefore, the absolute difference can be expressed as,

$$\frac{\sin\alpha.\cos\alpha.\sigma^2}{2}$$

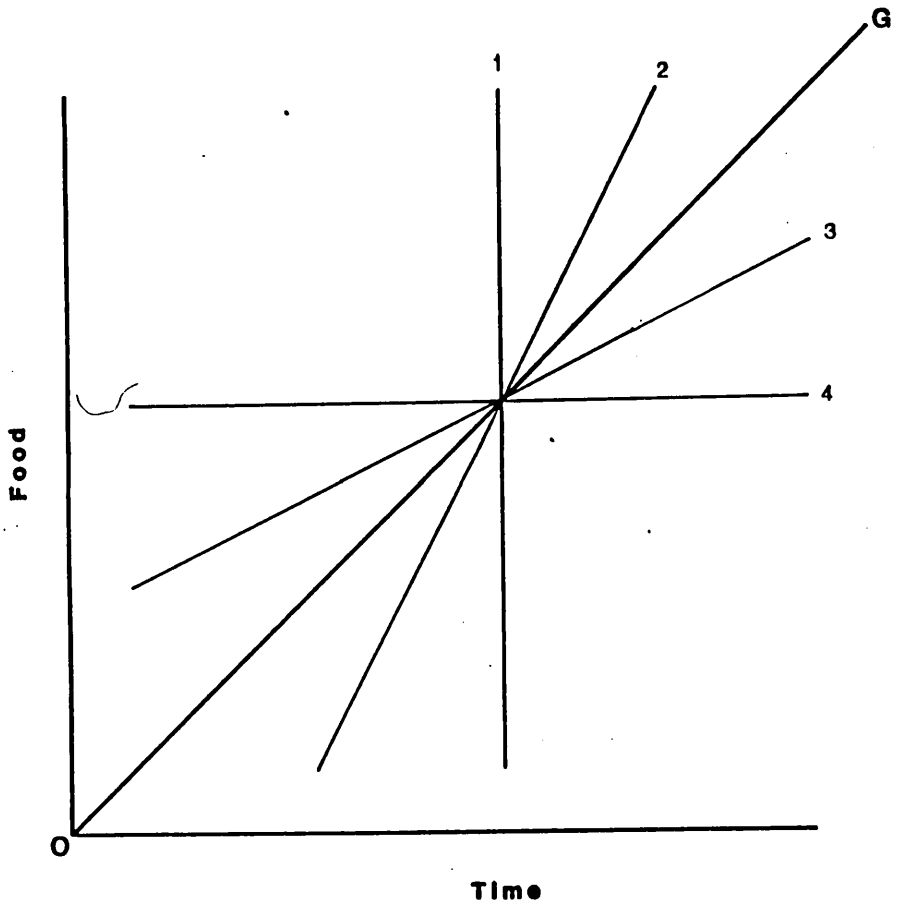
where σ^2 is the variance of the variable station.

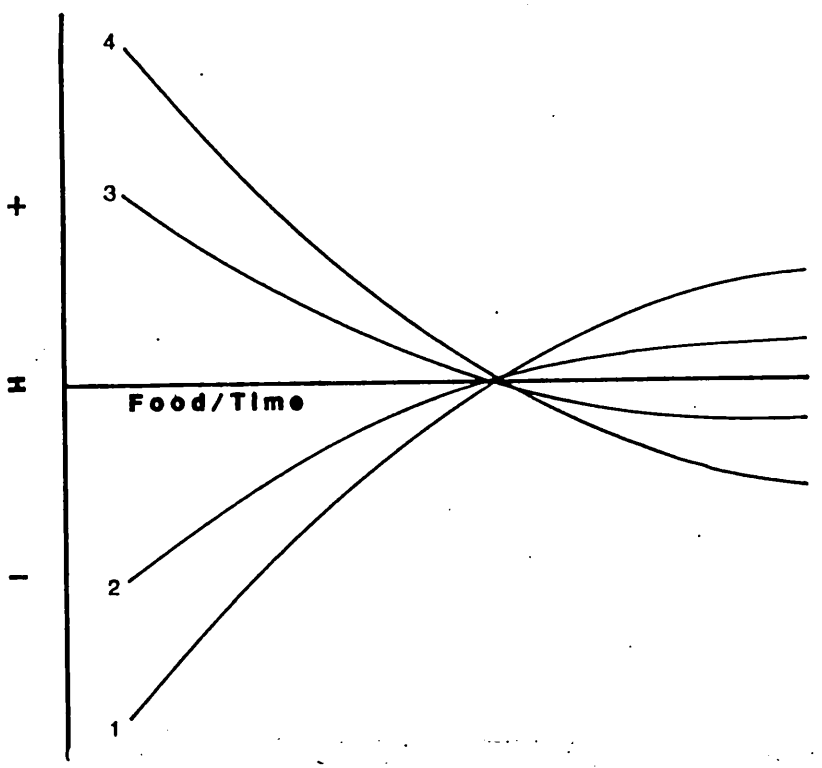
Figure 3 shows how expected hunger/satisfaction changes when food and delay are varied independently and together. The function is concave when food alone is varied so that hunger is minimised by choosing a constant station. When time alone is varied, the function becomes convex and a variable station should be preferred. When food and time are varied together, preference depends on the available feeding rate in relation to the budget line.

The model seems to accommodate the various empirical findings, (though see Barnard and Brown, 1985, discussed later in this chapter). It is simple, requiring only that the animal know how long it has been foraging and how long it has left to forage, and how much it has eaten and how much it has yet to eat. An animal may be thought of as asking itself, "If I obtain just enough food from now on to reach my goal on time, how much hunger/satisfaction will I experience?" This may seem an unlikely calculation, given that it ignores the animal's current performance. However, in the laboratory, although birds may go hungry during the experimental trials, they are usually fed at the end of the day.

Fig. 3

Model I: Change in expected hunger/satisfaction as food and delay are varied independently and together. Fig 3b shows how the axes in 3a, relating to food and time, translate into H with reference to the goal point G. Thus in 3a, if delay alone is manipulated (axis 4) then H measured at all points along the line with respect to G gives curve 4 in 3b. When delay is short, H is a large positive value becoming smaller with increasing delay until it eventually gives a negative value. The function is convex in shape and therefore variance should be preferred.
If reward size alone is manipulated (axis 1 in 3a) then the hunger function is concave (curve 1 in 3a) and variance should be avoided. When delay and size are manipulated together (axes 2 and 3 in 3a) then the shape of the hunger curve is convex when the feeding rate is less than the budget line and concave when the feeding rate is greater than that required by the budget.


G
1
2
3
4
Food
O
Time


4
3
+
H
Food/Time
2
-
1

Experimenters are careful to ensure their subjects' survival, and it is not unreasonable to suppose that the subjects themselves come to expect it. It is known that laboratory birds, regularly deprived of food in the afternoons, will compensate by eating more in the mornings (P. Clifton, unpublished observation). In a series of experiments, Collier and Rovee-Collier (see 1981, for a review) have shown that foraging behaviour is often very different in a closed economy (where the animal is permanently housed in the experimental apparatus and obtains all its food there) to that in an open economy (the typical laboratory context, where the animal obtains additonal food in its home cage). The assumptions of the model would seem to be fulfilled in the case of laboratory animals: they may also hold true for wild-living animals.

The model implies that risk sensitivity is a non-functional artefact of the animal's decision making mechanism. Perhaps "non-functional" is putting it too strongly, since there are circumstances in which this mechanism will enhance the probability of survival in the way envisaged by Caraco. Nevertheless, there are other circumstances in which minimising expected hunger will neither maximise intake rate nor minimise the probability of dying of starvation during the night. A functional argument in support of the mechanism must appeal to some other level: for example, the benefits gained through discounting the value of future rewards (discussed in more detail later in this chapter).

According to the model, an animal's response to variable food patches depends not only on its internal energy budget but on the form of the variability; in particular, whether the variability is one of time between food items, size of food items, or both. Caraco and others have shown that there is a theoretical functional advantage in responding to variance in different ways under different conditions. But, it has been argued above, they failed to demonstrate that "risk" proneness or aversion observed in the laboratory was functionally beneficial to the animals tested.

In addition it is not clear that the kind of choices Caraco gave his birds in the laboratory are those that face wild birds. It is hard to think of natural examples of birds choosing between different patches offering similar rates of feeding but with differing variability. Where variance differs between patches, it is likely that the mean rate of feeding will also vary. Barnard, Brown, MacNamara and Houston (1985) argue from mathematical assumptions that, to foraging shrews, differences in means are two orders of magnitude more important than variance

differences in their functional significance. If an animal finds itself in an environment that is unlikely to satisfy its food needs, it may be better to search for food patches that will satisfy them, rather than accept the given environment and attempt to make the best of a bad lot, especially if the most likely outcome is death through starvation. One would need to know whether the probability of starvation is greater when searching for good food patches or when exploiting a poor but variable food patch. It is not clear, therefore, how important it is, in a functional sense, for animals to be sensitive to risk. One of Caraco's own experiments casts doubt on the functional significance of risk sensitivity. He found (1982) that white-crowned sparrows were not any less risk averse than were smaller birds. He reasoned that they should be less averse to taking take risks because, being heavier and therefore having larger food reserves, they should be less constrained to meet strict energy budgets. If, in general, it is not very important to be sensitive to variance in feeding rate, then the model may be realistic both in the laboratory and in the wild.

3. WHEN TO LEAVE A FOOD PATCH. (MODEL-II)

3.a. In an environment of identical depleting patches

Model-I was developed to simulate evidence on risk sensitivity. With some modifications it can also mimic optimal foraging behaviour as predicted by marginal value theory (Charnov, 1976). At the simplest level, it may be seen from Fig. 2 that, given a sufficiently distant goal point G, an animal will prefer a large reward over a small one, and a reward with a short delay over one with a long delay because expected hunger is thus minimised. At a more sophisticated level, marginal value theory predicts that animals feeding in an environment of similar depleting patches should quit their current patch to travel to another when their instantaneous rate of feeding falls below the average rate for the environment (see Fig. 4). The foraging time within a patch is thus dependent on the travelling time between patches. Empirical evidence in support of MVT has come from Cowie (1977) showing that great tits stay longer in patches as the travelling time between them increases. This result, he claimed, was in quantitative as well qualitative agreement with MVT. (For recent reviews of tests of MVT see Krebs, Stephens and Sutherland, 1983; Krebs and Davies, 1984.)

Figure 5 shows one way (see Appendix 2 for another way) in which model-I can be modified to simulate Cowie's results. As in Fig. 2, the line OG represents the necessary rate of feeding for a bird foraging from dawn till dusk. In these experiments, the birds were starved for two hours before being allowed to forage in artificial trees containing pots of mealworm segments mixed in sawdust. Model-II assumes that birds sample the first patch (pot of mealworms) for some arbitrary time interval (say 10 sec). On the basis of its rate of feeding (including travelling time) in this patch, the bird makes a projection (represented as line AG_1) of how long it should take to get back on the course dictated by the budget line OG. For relatively rich patches, the new goal point (G_1) will be reached sooner than G_0. (What happens when patches are so poor that the daily budget cannot be met will be discussed later). The bird then travels to the next patch and leaves that patch when its expected satisfaction with reference to the new goal G_1 begins to decrease. In Fig. 5, the expected

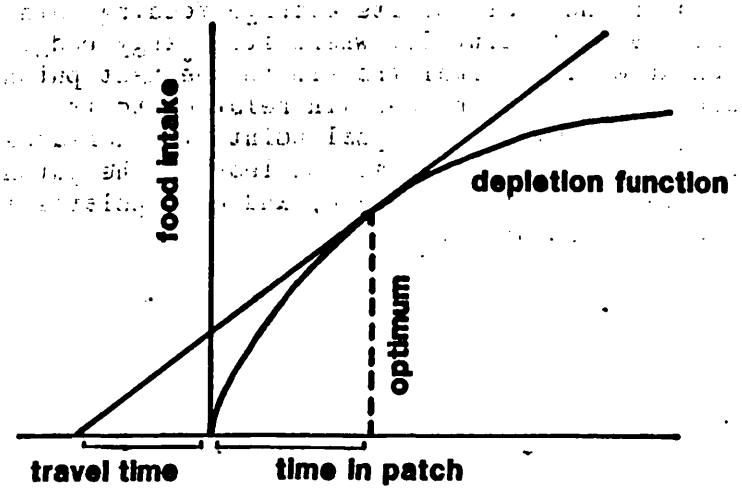
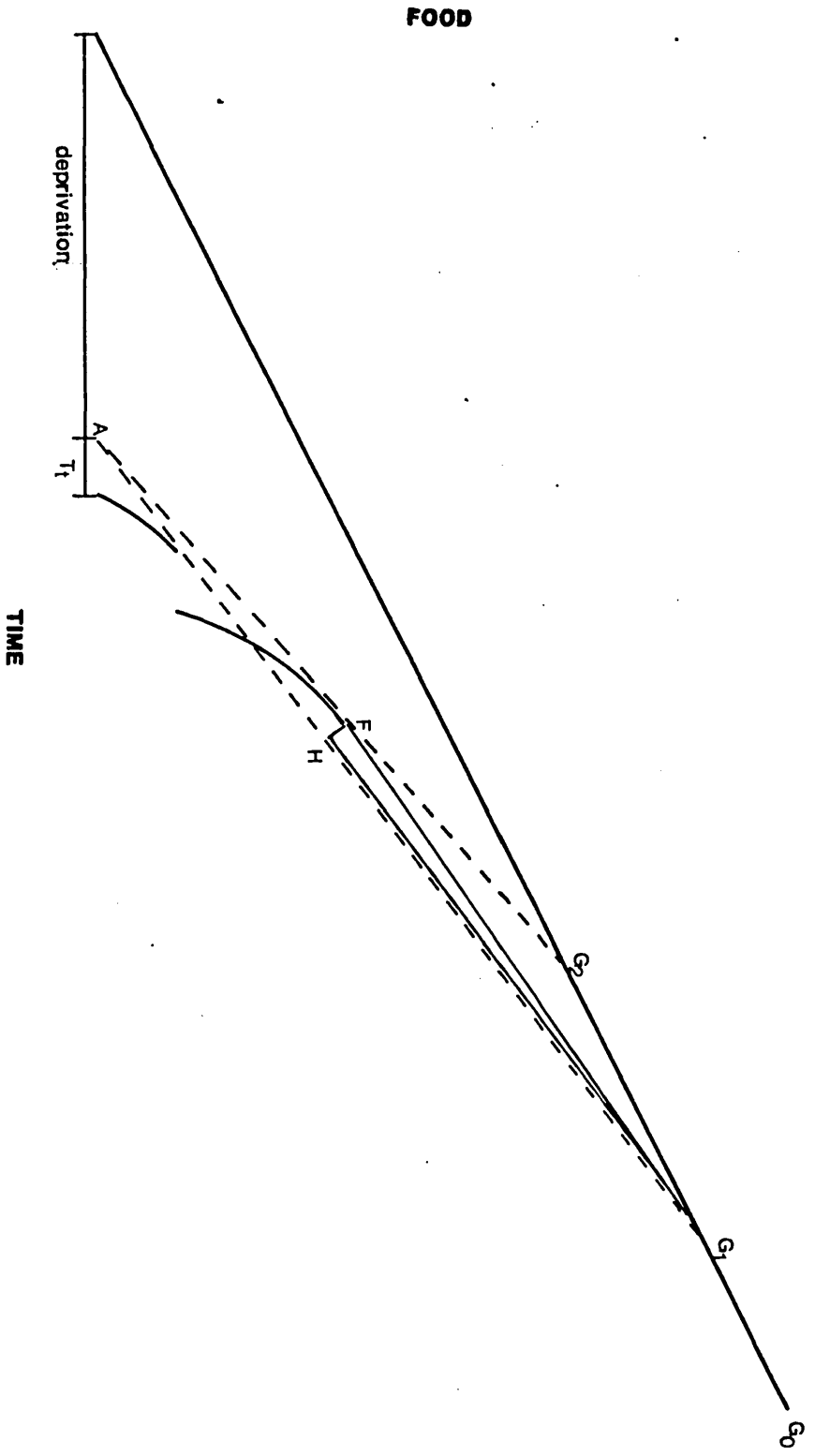


Fig. 4

The tangent method for solving the optimal time that an animal should stay in a patch of an environment consisting of identical depleting patches, each separated by a constant travelling time. The animal should leave a patch when its instantaneous feeding rate falls below the average feeding rate for the environment.

Fig. 5

Expected hunger model applied to the problem of how long to stay in a depleting patch, surrounded by other identical unexploited patches at identical distances. After a period of deprivation, the animal enters the environment at point A and travels T_t seconds to the first patch. It samples this patch for 10 sec, and on the basis of its average feeding rate thus far, sets itself a goal point G_1, where its energy budget would be in balance. The animal travels to the next patch and leaves it when its expected hunger (in relation to its average feeding rate AG_1 and its goal point G_1) increases, or its expected satisfaction decreases. On leaving the patch, it re-evaluates its average feeding rate, and extrapolates it to arrive at a new goal point G_2.


FOOD
deprivation
A
T_t
TIME
F
H
G_2
G_1
G_0

satisfaction at this point is depicted by $\Delta F_1G_1H_1$, i.e., satisfaction or hunger is evaluated with respect to average rate of feeding (AG_1) rather than the overall necessary daily rate (OG_o). (This has some consequences for the model-II's predictions of risk sensitivity which, again, will be discussed in the next section.) At this point (F_1), the bird re-evaluates its average feeding rate, and makes a new projection (AG_2). In this way, the bird gradually improves upon its feeding rate until no further improvement is possible, at which point it is spending the optimal foraging time per patch for a given travelling time between patches. The modified model requires that the animal adjust its goal point after each patch visit, in line with its average feeding rate.

This process can be modelled mathematically using data from Cowie (1977). He found that the rate of feeding declined exponentially and the amount of food eaten for a given time in a patch was well described by the function,

$$F.(1-\exp(-v.t)) \qquad (3.1)$$

where F is a constant representing total amount of food available (from Cowie's data, 6.538); v is a constant representing the exploitation rate (0.0081) and t is the time spent feeding in the patch. (Note that this relationship is a smooth, continuous approximation of what is really a stochastic process; in reality, food comes in discrete packages interspersed with periods where no food is found.) Substituting (3.1) for y in equation (2.2). and bringing travelling time (t_t) into the equation gives us,

$$H = \frac{1}{2}.\frac{[(F(1-\exp(-v.t)).T - (t+t_t).Y].[Y^2-(F(1-\exp(-v.t)) + T^2-(t + t_t).T]}{T^2 + Y^2} \qquad (3.2)$$

The instantaneous rate of change of H with t is given by,

$$\frac{dH}{dt_n} = [[(T.F.v.\exp(1-v.t) - Y).(Y^2-(F(1-\exp(-v.t)) + T^2-(t + t_t).T] + [(-Y.F.v.\exp(-v.t) - T).(F(1-\exp(-v.t).T - (t + t_t).Y]].\frac{1}{2}.\frac{1}{T^2+Y^2} \qquad (3.3)$$

Maximum satisfaction (or minimum hunger) occurs when dH/dt = 0. The value of t at this point can be found by computer iteration (Newton-Raphson). (An arbitrary value of t is inserted into the functions, dH/dt and d^2H/dt^2. A new estimate of t (t_2) is then obtained from $t_2 = t - (dH/dt)/(d^2H/dt^2)$, and this value is inserted again into the above functions to produce a new estimate. The iteration is halted when the difference between successive

extimates of t_n falls below some specified level - 0.001 sec in the simulations that follow).

Table 1 shows that birds minimising expected hunger in the way described in Fig. 5 will, as experience in the environment increases, tend to stay the optimal patch time (as determined by MVT). In order to make these results comparable with Ollason (1980) who has also developed a learning model of foraging behaviour, Table 1 makes use of the same range of t_ts and employs the same criterion (± .01 sec, between successive patch residence times) for determining the point at which patch residence times reach equilibrium. Although a direct comparison with Ollason's model is not possible (because there are some variables unique to the different models), animals following the expected hunger model-II are quicker to settle down to a constant patch time than are Ollason's animals, and the residence times are closer to the optimum. In both models, increasing memory span (or k in Ollason's model) makes little difference to the equilibrium residence time, but the bird has to visit more patches before this point is reached. The expected hunger/satisfaction model is generally better than Ollason's, both in the closeness of the equilibrium t_n to the optimal residence time and in the speed of its convergence. In this environment where all patches are the same, the expected hunger model can converge on the optimium residence time within 5 patch visits.

Table 1. Comparison of the equilibrium residence times (sec) obtained using expected expected hunger model-II with Ollason (1980) and the optimal foraging strategy.

	Expected Hunger Model-II		Ollason (1980)		Optimum
	memory span		k		
	last patch	all patches	100	6400	
t_t					
4	30,15	30,47	28,50	31,92	30,15
8	41,93	42,04	38,68	40,57	41,93
12	50,71	50,90	45,88	49,60	50,71
16	57,94	58,18	51,54	56,96	57,94
20	64,19	64,48	56,24	63,29	64,19
24	69,74	70,08	60,26	68,89	69,74
28	74,78	75,14	63,75	73,94	74,77
32	79,39	79,78	66,86	78,58	79,38
36	83,66	84,08	69,63	82,86	83,66
n	5	31	10	297	

The bird has been starved for 7200 sec before foraging begins, and needs to find 0,01 bits of food per second - an achievable goal in these experiments. The equilibrium values of t_n are obtained by presenting the 'bird' with a series of identical repeating patches (where F=6,538, v=0,0081) separated by a constant travelling time (t_t). The first patch is sampled for 10 sec and the "bird" sets it's goal point (see Fig. 5) on the basis of this experience. In subsequent patches the goal point is reset according to its experience in the most recent patch or else its total feeding experience in the environment. The bird continues foraging until residence time in the nth patch differs from that in patch n-1 by no more than 0,01 sec. After Ollason (1980), a measure of the speed of convergence of t_n to its equilibrium was obtained by allowing the model to equilibriate with t_t=4, and the corresponding t_n was then used as the initial sampling time for the other environments in which t_t varied from 8-36 sec. The bottom row shows the average number (n) of patches visited before t_n converged to equilibrium. The variable "k" in Ollason's model is related to the animal's rate of forgetting; when k is small, recent events loom larger in the memory than when k is big.

3.b. In a mixed environment of depleting patches

In an environment where the quality of patches is variable and the animal cannot assess their quality without first sampling them, then MVT says that an animal should leave a patch when its marginal rate of feeding falls below the average rate for the environment as a whole. In the following simulations model-II was presented with an environment containing equal numbers of three patch types differing in the amount of food they contained (F) and/or their exploitation rates (v).

Environment 1 consisted of 999 patches, separated by 20 sec travelling time, each containing 6 food units. Equal numbers (333) of patches had exploitation rates of 0.007, 0.008 and 0.009. In environment 2, all patches had the same exploitation rate (0.008) but differed in the amount of food they contained (4, 6 or 8 units). In the third environment, total food and exploitation rates for the three patch types were F = 4, v = 0.007; F = 6, v = .008, and F = 8, v = .009, and in another variation of this environment total food and exploitation rates were F = 4, v = .005; F = 6, v = .008, and F = 8, v = .011. The optimal marginal feeding rate which determines when a bird should leave a given patch in a given environment was calculated as follows.

The optimal solution (MVT)

If a bird leaves a patch when its marginal (ie instantaneous) feeding rate within a patch falls below some rate (r_m), then its average rate of feeding (r_a), is the amount of food obtained within the patch divided by residence time plus travelling time. The marginal rate of feeding (r_m) within a patch is given by differentiating equation (3.1) with respect to time,

$$r_m = F.v.e^{-v.t},$$

The time spent in the patch will be,

$$t = -\ln(r_m.F^{-1}.v^{-1}).v^{-1},$$

and the amount of food obtained (a) is given by equation (3.1)

$$a = F.(1 - e^{-v.t})$$

which, on substituting for t, gives,

$$a = F - r_m.v^{-1}.$$

For an environment containing three patch types separated by equal travelling times (t_t), the average rate of feeding for a given r_m is,

$$r_a = \frac{a_1 + a_2 + a_3}{t_1 + t_2 + t_3 + 3.t_t}$$

The problem is to find a single r_m which results in the best average feeding rate r_a. This occurs when $r_m = r_a$. That is, when,

$$0 = \frac{\sum_{i=1}^{3} F_i - r_m.v_i^{-1}}{\left[\sum_{i=1}^{3} \ln(r_m.F_i^{-1}.v_i^{-1}) + t_t\right]} - r_m \qquad (3.4)$$

This equation can be solved for r_m by computer iteration as described earlier.

In order to arrive at this optimal r_m, a bird would have to know in advance that there are three patch types, that they occur in equal numbers, and that they are separated by equal patch times. It would also need to know the particular qualities (F and v) of each type. This is not a very realistic set of assumptions.

The average feeding rate solution

If we assume that birds is aware only of its average feeding rate (r_a) within an environment and that it is able to monitor this rate from moment to moment, then a good leaving rule is to leave a patch whenever r_a begins to fall. In an environment where all patches are the same and are separated by the same travelling time (see previous section, 3a), then this rule results in birds staying the optimum residence time: it is exactly equivalent to the tangent solution of the Marginal Value Theorem suggested by Charnov (1976b). In an environment where patches differ in quality, the average rate model will no longer produce the best feeding rate. The difference between this average rate model and the optimal solution described above is that the optimal solution requires a bird to leave a patch when its marginal feeding rate (r_m) falls below the best achievable rate for the environment as a whole. The average rate model requires the animal to leave a patch whenever the overall feeding rate experienced in the environment upt to the present time begins to fall. The point of departure will therefore depend on the bird's actual feeding experience, rather than a mathematically derived ideal.

For a bird which continuously monitors its average rate of feeding and leaves a patch when this rate begins to fall, then since average rate is given by,

$$r_a = \frac{F_i.(1-\exp(-v_i.t)) + a_{n-1}}{t + t_t + t_{n-1}}$$

(where a_{n-1} is total food consumed from previous patches, and t_{n-1} is total time spent in the environment up to leaving the previous patch), the bird should leave when $dr_a/dt = 0$, ie when,

$$0 = \frac{(t + t_t + t_{n-1}).(F_i.v_i.\exp(-v_i.t)) - (F_i.(1-\exp(-v_i.t)) + a_{n-1})}{(t + t_t + t_{n-1})^2} \qquad (3.5)$$

The best-fixed-residence-time solution

Another rule which animals could use in deciding when to leave a patch is simply to leave all patches, regardless of quality, after a given residence time. The problem is to find a single residence time, applicable to all patches, resulting in the best feeding rate. In an environment containing equal numbers of three patch types, the optimal residence time may be found averaging the respective depletion functions, and calculations performed as for section 3a. Thus,

$$a = \frac{\sum_{i=1}^{3} F_i.(1-\exp(-v_i.t))}{i}$$

$$r_m = \frac{da}{dt} = \frac{\sum_{i=1}^{3} F_i.v_i.\exp(-v_i.t)}{i}$$

$$ra = \frac{a}{(t+t_t)}$$

Since residence time (t) is optimal when $r_a = r_m$, then,

$$0 = \frac{(t+t_t).(\sum_{i=1}^{3} F_i.v_i.\exp(-v_i.t)) - (\sum_{i=1}^{3} F_i.(1-\exp(-v_i.t)))}{i} \qquad (3.6)$$

which may be solved for t using computer iteration. For a real bird, a residence time rule would have to be learned in the course of foraging, and it would only gradually approach the optimum. The overall feeding rate would therefore be poorer than the optimum shown in Table 2.

Table 2 compares the models' performances in the three environments with the optimal achievable performance. A fourth environment is also included where F and v are constant (6 and .008) but travelling time between patches is either 10, 20 or 30 sec. As in the previous section

both expected hunger and average rate models come very close to optimal achievable performance but the average rate model does slightly better in all but environment 3b, where patch quality is most variable. Both models do better in most environments than the maximum achievable rate using a residence time rule, and this difference would be more pronounced where residence time was learned during the course of foraging. As patch quality becomes more variable, the single fixed residence time rule performs increasingly badly, compared with models which dictate different residence times according to patch quality.

Table 2. The models' performances in three environments of mixed depleting patches, and one environment with variable travelling times, compared with optimal performance, given by MVT and that using a fixed residence time rule.

	Rate of feeding (food units/sec)			
	Expected Hunger Model-II	Average Rate Model	Optimum (MVT)	Best Fixed Residence Time (t)
Environment 1 (variable v)	,0284945	,0286183	,0286187	,0285635 (64,3847 sec)
Environment 2 (variable F)	,0304390	,0304719	,0304765	,0286223 (64,627 sec)
Environment 3a (variable v and F)	,0320384	,0320906	,0320962	,0291729 (63,461 sec)
3b	,0350885	,0350667	,0351516	,0299551 (60,167 sec)
Environment 4 (variable t_t)	,0285989	,0286217	,0286223	,0286223 (64,627 sec)

Each of the first three environments consisted of 999 patches (333 of each patch type) encountered in random order, and separated by 20 sec travelling time. In Environment 1, F was always 6, and v was ,007, ,008 or ,009. In environment 2, v was always ,008 and F was 4, 6 or 8. In Environment 3a F = 4 and v = ,007; F = 6 and v = ,008; or F = 8 and v = ,009; in environment 3b F = 4 and v = ,005; F = 6 and v = ,008; or F = 8 and v = ,011. In the fourth environment F was 6, v was ,008, and the travelling times were either 10, 20 or 30 sec. Parameters of the model were as for Table 1. The feeding rates for the constant residence time model are those achieved by "birds" staying the fixed time, shown in brackets, for all patches. For calculation of optimal feeding rates for the other models see text.

3.c. In an environment where food-size and search time are variable.

In the previous simulations, it has been assumed that the amount of food eaten in a patch is a continuous function of a bird's residence time there. For many foraging animals however, food comes in discrete bits of varying size and at varying intervals. Model-II may be easily adapted to a more stochastic environment. In the following simulations, birds are once again presented with exponentially depleting patches but food items occur in discrete units at particular times. On average, when a bird first enters a patch, food items are large but with increasing residence time in a patch, they become smaller. This relationship is stochastic rather than deterministic, so that many food items may be larger than preceding items, although the general trend is toward successively smaller sizes. In particular, all birds received some kind of food item at a random intervals between 0 and 10 sec; on average, every 5 sec. The size of food items was dictated by the depletion function characterising patch quality (see Fig. 6). The size of the first item varied randomly between values appropriate for a bird feeding for 0 to 10 sec in a continuously depleting patch. The size of the second item ensured that the bird had eaten the equivalent of a bird foraging in a continuously depleting patch for 5 to 15 sec, and so on. This means, for example, that a bird may have had to wait up to 10 sec for its first find, while the size of the find may have been equivalent to less than 1 sec of foraging time in a patch where feeding rate is a perfectly continuous function of residence time. Likewise, it may have found a food item in less than one second with a size value appropriate to nearly 10 sec foraging in a continuously depleting patch.

When foraging in a particular patch, birds reviewed their prospects every time they discovered a new food item. If they decided to leave for another patch they left immediately or else remained in the patch until another item was found. On average therefore, they reviewed their situation every 5 sec. In early simulations birds left whenever expected hunger increased or average feeding rate decreased relative to expected hunger or average rate on finding the previous food item. For both models, however, this resulted in birds leaving patches earlier than was optimal. Both models performed better when the bird left after two successive falls

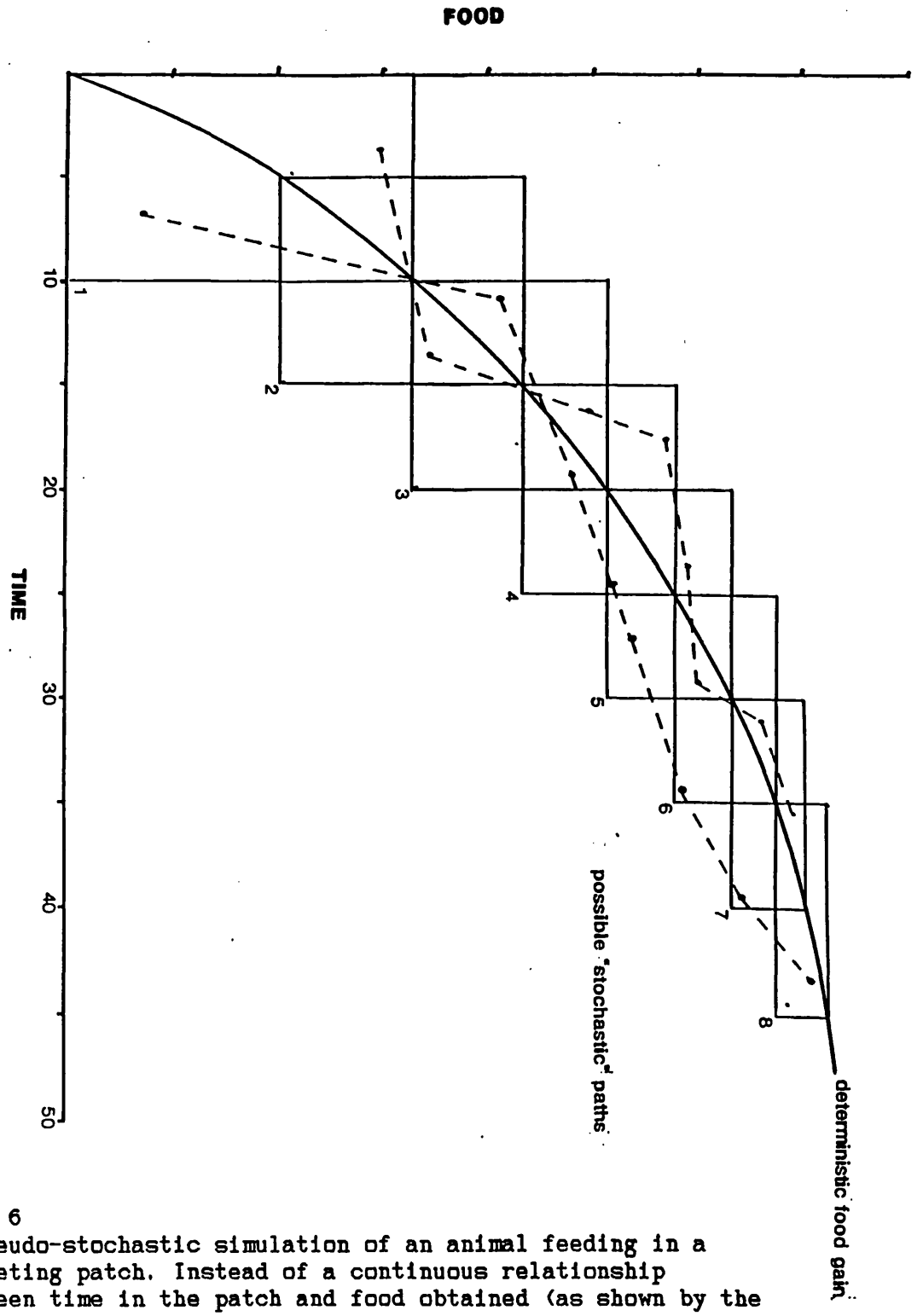


Fig. 6
A pseudo-stochastic simulation of an animal feeding in a depleting patch. Instead of a continuous relationship between time in the patch and food obtained (as shown by the deterministic curve), animals receive discrete bits of food of varying sizes at varying times. The sizes of the bits tend to get smaller as the animal stays longer in the patch, but occasionally the trend may reversed so that a large food item follows a small one.

in feeding prospects. Performance of the expected hunger model was further improved by weighting the average expected hunger (H) with the H associated with the previous find in the patch. Thus,

$$Hw_n = W.Hw_{n-1} + H_n$$

where Hw_n is the weighted expected hunger for the nth food find and W is the weighting factor. The bird leaves a patch when $Hw_n > Hw_{n-1} > Hw_{n-2}$. Performance of the average rate model was similarly improved by a weighting factor, such that,

$$Yw_n = W.Yw_{n-1} + Y_n$$

$$Tw_n = W.Tw_{n-1} + T_n$$

$$Rw_n = \frac{Yw_n}{Tw_n}$$

where Y_n is total food eaten in the environment including the nth food find; T_n is total time spent in the environment up to finding the nth food find. The bird leaves a patch when weighted average rate $Rw_n < Rw_{n-1} < Rw_{n-2}$. After some experimenting, a weighting factor (W) of 0.5 was used for both models. This seemed to produce the best results in both cases but no rigorous attempt was made to find the optimal W, or to assess different weighting methods. Table 3 shows the models' performances in the environments described in the previous section. Both models performed less well under these stochastic conditions compared with the deterministic environments of the previous simulations (part b). Feeding rates worsened in comparison with the optimum, as patch qualities became more variable (environments 3a and 3b). Under these circumstances, the optimal foraging strategy is to spend little or no time in the worst patches, whereas the leaving rules employed by the models used here, require that birds stay until at least three food items have been found. Under stochastic conditions, the unweighted expected hunger model performed slightly better than the average rate model in environments 1 and 2 and slightly worse in environments 3a and 3b, but the differences were not significant. Weighted models performed slightly, but significantly, better ($p < .001$) than their unweighted variants,

Feeding rates ranged from 89 to 96% of the optimal achievable rates. This might seem to indicate a respectable performance for all the variants, but for stressed animals feeding in poor environments over many weeks (e.g. birds in a hard winter) small differences in daily feeding rates can lead to large differences in mortality (McNamara and Houston,

1982). On the other hand Janetos and Cole (1981) have argued that sub-optimal, yet simple, foraging rules may have a selective advantage over more complex, albeit "optimal," rules which require the evolution of more sophisticated and more expensive information processing hardware. It is therefore difficult to assess the relative merits of the different models and their variants, because, although we know their relative advantages in terms of feeding rates, we do not know the evolutionary costs of supporting them.

Table 3. The models' performances in three "stochastic" environments of mixed depleting patches, compared with the theoretically optimal performance, given by MVT and that using a fixed residence time rule.

	Rate of feeding (food units/sec)			
	Expected Hunger Model-II	Average Rate Model	Optimum (MVT)	Best Fixed Residence Time (t)
Environment 1 (variable v)	,0275675	,0269618	,0286187	,0285635 (64,3847 sec)
(unweighted)	(,026610)	(,0265984)		
Environment 2 (variable F)	,0289596	,0284989	,0304765	,0286223 (64,627 sec)
(unweighted)	(,0277447)	(,0277190)		
Environment 3a (variable v and F)	,0299842	,0298415	,0320962	,0291729 (63,461 sec)
(unweighted)	(,0289152)	(,0289902)		
3b	,0319062	,0323533	,0351516	,0299551 (60,167 sec)
(unweighted)	(,0315509)	(,0316027)		

Food was obtained in discrete units of variable size and at variable intervals in a pseudo-stochastic manner described in the text. Each of the first three environments consisted of 999 patches (333 of each patch type) encountered in random order, and separated by 20 sec travelling time. In Environment 1, F was always 6, and v was ,007, ,008 or ,009. In environment 2, v was always ,008 and F was 4, 6 or 8. In Environment 3a F = 4 and v = ,007; F = 6 and v = ,008; or F = 8 and v = ,009; in environment 3b F = 4 and v = ,005; F = 6 and v = ,008; or F = 8 and v = ,011. Parameters of the model were as for Table 2. The weighting factor W (see text) was 0,5. Results obtained without using a weighting factor are shown in brackets. Appendix 2 presents results in these environments for another variant of the expected hunger model.

3.d. In an environment where patches are revisited

So far, we have considered foraging strategies in environments where birds could choose to continue feeding in a patch or leave it to travel to a new one. The optimal policy in these cases was to leave all patches, regardless of their particular qualities, when the marginal feeding rate fell below some fixed criterion. Such a policy would not be optimal where birds are obliged to revisit patches. Consider, for example, an environment of only two identically depleting patches. Having spent t sec in patch 1 and now feeding in patch 2, it is clear that a bird should stay longer than t sec in this patch, since after t sec, patch 2 is identical to patch 1. And it is wasteful to incur the cost of travelling to patch 1 if the prospects there are no better than the prospects in the current patch (2).

In more detail, we already know from (3.6) that the optimal residence time (t_1) in an environment of identical exponentially depleting patches satisfies the following equation,

$$F.v.\exp(-v.t_1) = \frac{F.(1-\exp(-v.t_1))}{t_t + t_1}$$

which on rearranging becomes,

$$0 = \frac{\exp(v.t_1)}{v} - \frac{1}{v} - t_t - t_1 \qquad (3.7)$$

The residence time t_1 is optimal for the first patch in this environment. The optimal residence time in the second patch (t_2) satisfies equation (3.8), where the instantaneous feeding rate on leaving this patch equals the extra food obtained in this patch, divided by the extra time required to obtain it, plus travelling time.

$$F.v.\exp(-v.t_2) = \frac{F.(1-\exp(-v.t_2)) - F.(1-\exp(-v.t_1))}{t_t + t_2 - t_1}$$

which on rearranging becomes,

$$0 = \frac{\exp(v.(t_2 - t_1))}{v} - \frac{1}{v} - t_t - (t_2 - t_1) \qquad (3.8)$$

From (2.7) we can substitute for 0 in (2.8) giving,

$$\frac{\exp(v.t_1)}{v} - \frac{1}{v} - t_t - t_1 = \frac{\exp(v.(t_2 - t_1))}{v} - \frac{1}{v} - t_t - (t_2 - t_1)$$

which on rearranging becomes,

$$t_2 = \frac{\exp(v.(t_2 - t_1))}{v} - \frac{\exp(v.t_1)}{v} + 2.t_1$$

and therefore,

$$t_2 = 2.t_1$$

Thus, in an environment of two identical exponentially depleting patches, the bird should spend twice as long in the second patch as the residence time spent in the first. On leaving the second patch, the bird is obliged to revisit the first patch, where it has already fed for t_1 sec. The optimal residence time (t_3) must take this into account. Thus,

$$0 = \frac{\exp(v.(t_3 + t_1 - t_2))}{v} - \frac{1}{v} - t_4 - (t_3 + t_1 - t_2)$$

which, on substituting (2.7) for 0 and rearranging, becomes,

$$t_3 = \frac{\exp(v.(t_3 + t_1 - t_2))}{v} - \frac{\exp(v.t_1)}{v} + t_2$$

$$t_3 = t_2$$

In this environment therefore, the optimal residence time for the first patch visit is the same as that in an environment of many identical patches (given by equation (3.7)). On all subsequent visits, including revisits, birds should spend twice this time foraging within patches.

There is no mechanism in either the expected hunger or average rate models that allows a bird to take account of the fact that a patch has already been visited and we may expect therefore that birds behaving in accordance with these models will leave patches after sub-optimal residence times. Table 4 shows that this is indeed the case.

It may be seen that birds following expected hunger or average rate models will stay for increasingly shorter times with subsequent visits. This leads to a poorer rate of feeding than that achieved by the optimal strategy.

In contrast to environments with many patches, in environments where patches must be revisited, both models perform less than optimally. But how well does the model's sub-optimal performance reflect the behaviour of living birds ? As far as I am aware, there are no data in the literature on residence times in environments where patches must be revisited. However, I have performed an experiment where bullfinches were obliged to revisit two depleting patches and we may compare their residence times with the optimal residence times and those predicted by the expected hunger and average rate models. In this experiment, patch depletion was best described by a power function of the sort, $y = a.t^b$, where y is the amount of food obtained in residence time t, and a and b are constants. The optimal residence time in the first patch satisfies the equation,

Table 4. Residence times generated by expected hunger and current rate models, compared with optimal times, in an environment of two identical exponentially depleting patches.

	Models		
	Exp. Hunger-II	Average Rate	Optimal
Patch/Visit			
1/1	64.627	64.627	64.627
2/1	64.627	64.627	129.254
1/2	0.059	13.463	129.254
2/2	14.013	23.855	129.254
1/3	25.179	19.394	129.254
2/3	19.552	16.960	129.254
1/4	16.026	15.121	129.254
2/4	14.775	13.700	129.254
1/5	13.542	12.562	129.254
2/5	12.441	11.626	129.254

Residence times (in seconds) are for exponentially depleting patches (where F=6 and v=.008) separated by 20 sec travelling times.

$$a.b.t_1^{b-1} = \frac{a.t_1^b}{t_t + t_1}$$

so that,

$$t_1 = \frac{t_t.b}{(1-b)}$$

For the second patch, optimal residence time (t_2) is given by,

$$0 = \frac{t_2}{b} - \frac{t_1^b}{b.t_2^{b-1}} - t_t - (t_2 - t_1)$$

which may be solved by iteration. Optimal residence time for the third patch (t_3) visit must take account of the fact that this patch has already been visited. It must satisfy the equation,

$$0 = \frac{t_3 + t_1}{b} - \frac{t_2^b}{b.(t_3 + t_1)^{b-1}} - t_t - (t_3 + t_1 - t_2)$$

and subsequent visits must similarly take account of the time already spent feeding in the patch concerned. Table 5 compares optimal residence times with model-generated times and actual residence times for a particular bullfinch.

Table 5, Optimal residence times (sec) in a 2-patch environment (depleting according to a power function) compared with model-generated times and actual residence times observed with a live bird.

	Models			
Patch/Visit	Exp. Hunger-II	Average Rate	Optimal	Actual
1/1	59,532	59,532	59,532	173,806
2/1	59,532	59,532	208,290	214,731
1/2	0,102	32,187	382,885	85,600
2/2	35,660	60,913	552,686	102,917
1/3	70,816	58,258	721,082	64,000
2/3	59,568	59,096	888,738	
1/4	52,307	59,191	1055,918	
2/4	57,927	59,288	1222,794	
1/5	59,317	59,347	1389,444	
2/5	58,720	59,387	1555,900	

The depletion function ($0{,}509 \cdot t^{-72132}$) was taken from data for one bird whose behaviour was typical of a larger group of four birds. Average residence times (calculated for 32 trials) are given for the first four patch visits, and, since further uninterrupted visits were relatively infrequent, the fifth value represents the average for the fifth and successive visits. Travelling time between patches was 23 sec.

The optimal policy in this environment is to spend increasingly longer times foraging in successive patches, whereas the model birds, after initial fluctuations, settle on a constant foraging time, close to the optimal time for the first patch visit. The observed residence times for a real bird more closely resemble the model birds than the optimal bird, but the data are too variable to draw any confident conclusions and the correspondence is poor for the first patch visits. There may be reasons, consistent with the models, why the live bird spent longer than expected in the first patches. If, for example, in the expected hunger model, the bird based its decision to leave the first patch of a trial on its experienced feeding rate for the whole of the previous trial, it would certainly stay longer than the optimum, since initial feeding rates will be higher than those achieved towards the end of a trial. (The values in the table, assume that the bird spends the optimal time in the first patch.)

It is clear, nevertheless, that the bird's behaviour was radically different from the optimal foraging times.

It has been shown in this section, that in a variety of circumstances, the expected hunger model-II results in nearly optimal foraging behaviour, and that where it results in sub-optimal behaviour, there is evidence that bullfinches behave in a similarly sub-optimal way. The average rate model makes very similar predictions, but this is not surprising, as it is shares similarities with the EH model-II. Both models in fact make use of a bird's average feeding rate. The EH model-II uses the average feeding rate on leaving a patch to set a new goal point; the animal leaves the next patch when its expected hunger in relation to the new goal point begins to increase. The average rate model simply leaves whenever the overall rate of feeding begins to fall. The former, though more complex has the adavantage, shown in section 1, of generating preferences between patches of different variances. (The extra complexity is only a small handicap to its performance as a forager in depleting patches.) We return to the discussion of risk preference in the next section.

4. RISK SENSITIVITY REVISITED

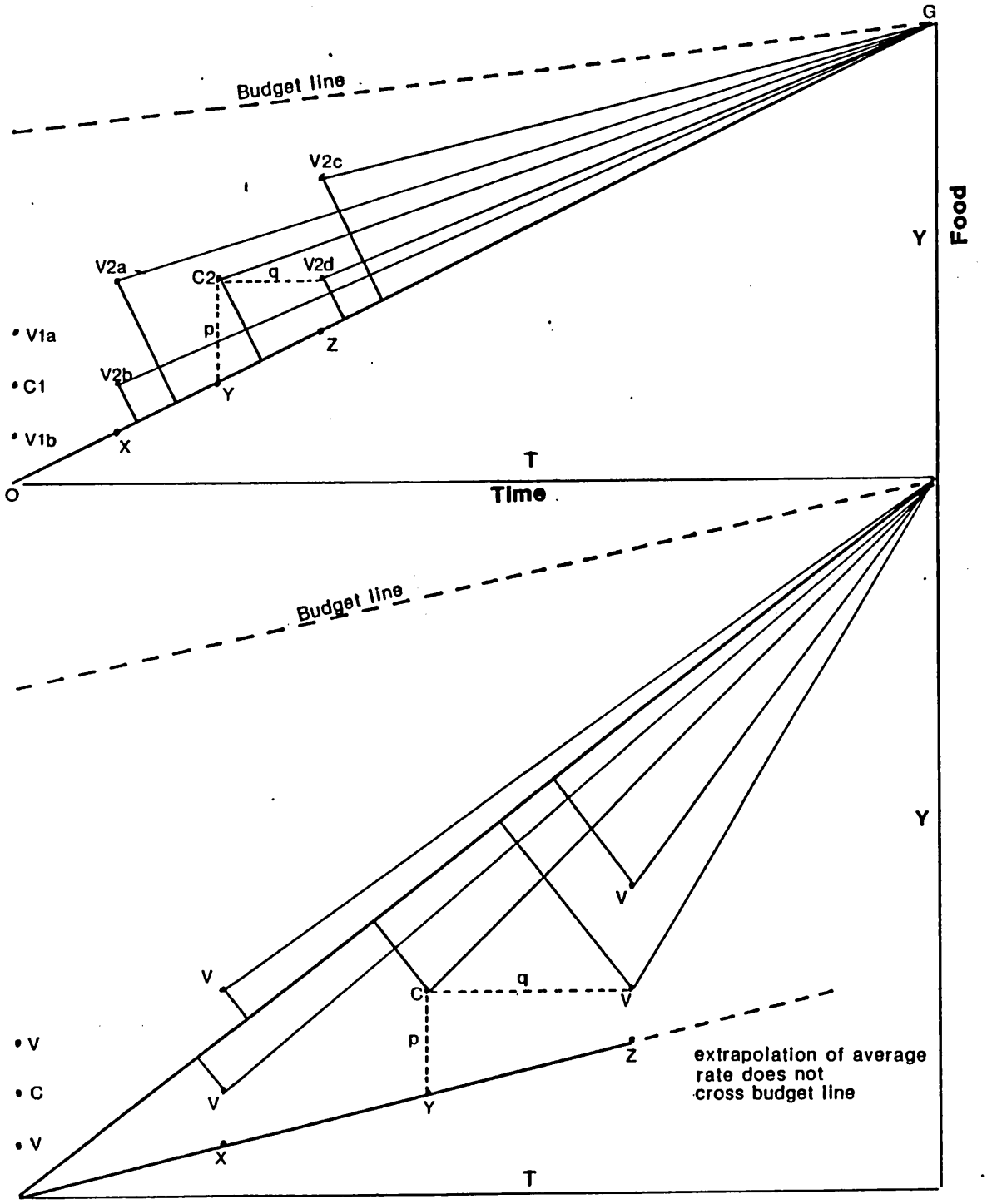
4.a. Performance of the modified model -- EH-II

For the expected hunger model to perform more or less optimally in an environment of depleting patches, the model (EH-I), as described in section 1, had to be modified (EH-II). This has consequences for its sensitivity to variance.

In the EH-II version, an animal's goal point is given by extrapolating its current rate of feeding to the point where it meets the budget line. Its expected hunger or satisfaction is calculated with reference to its current feeding rate and the extrapolated goal point (see Fig. 5). An animal, currently below its budget line, but feeding in a relatively rich environment, will show a preference for patches where intervals between food items are variable and for patches where the size of food items is constant. In this respect the modified EH-II model behaves exactly the same as the original EH-I version. However, when food size and interval are manipulated together, the modified model would seem to predict that an animal will show no preference between a variable patch and a constant one giving the same mean feeding rate. The reason for this is shown in Figure 7. Since an animal gauges its hunger in terms of its deviation from the current average feeding rate, and since the feeding rate at the end of a given trial is always constant regardless of the patch chosen, then expected hunger will always be zero at the end of every trial (shown as points X, Y, and Z in Fig. 7a). Given, however, that food comes in discrete bits at particular times, the feeding rate within a trial will not be constant, and in a variable patch, will sometimes be greater and sometimes smaller than that obtainable in a constant patch. If we assume that an animal evaluates a trial (and therefore the patch) on the basis of its experience within a trial, rather than its position at the end of a trial, then the model will again generate risk-sensitive preferences. Appendix 3 shows this to be true for animals which base their preferences on the average expected hunger integrated over the whole trial. The same point is made here for a simpler case. Take, for example, the kind of experiment performed by Caraco. At the constant station birds received two bits of food followed by a two-minute delay before the next trial: at the variable

Fig. 7

Risk sensitivity of the modified expected hunger model.
a) Where rate of feeding is sufficient to achieve energy balance. Expected hunger in the modified version II is assessed with reference to the average feeding rate rather than the budget line. Thus, when food and delay are manipulated together and proportionally, the average feeding rate at the end of a trial will be the same regardless of whether or not the animal chose the constant (Y) or variable (X, Z) station, and expected hunger/satisfaction (H) will be zero in each case. This implies that the animal should be indifferent between stations. However, if we assume that the animal bases its foraging decisions on the relative hunger it experiences during a trial then preferences surface again. Suppose, for example, the animal assesses H as soon as it receives a food item. At the beginning of trial 1, the constant station (C_1) will be preferred to the variable station (V_{1a} and V_{1b}) since, at this stage, only food size has been varied. Upon receiving food items in trial 2, the animal which always chooses the constant patch will be at point C_2, whereas the animal which always chooses the variable patch may find itself at one of four points, V_{2a}, V_{2b}, V_{2c} or V_{2d}. The average expected satisfaction is less for birds choosing the variable patch.
b) Where rate of feeding is less than that required by the energy budget. At the beginning of trial 1, expected hunger is again minimised by choosing the constant patch. Upon receiving food items in trial 2, expected hunger is now minimised by choosing the variable station.


G
Budget line
V2c
Y
Food
V2a
C2
q
V2d
p
Z
• V1a
V2b
• C1
Y
• V1b
X
T
O
Time
Budget line
Y
V
V
C
q
V
p
Z
• V
• C
• V
V
Y
X
T
extrapolation of average
rate does not
cross budget line

station they received either one bit of food and a one-minute delay or three bits of food and a three-minute delay. If we assume that birds judge the stations according to the hunger expected immediately upon receiving a food item, then they will prefer the constant patch since food is obtained at the same time (i.e. as soon as the trial begins, points V1a, V1b and C1 in Fig. 7a) irrespective of which patch is chosen, and we already know that the model bird prefers patches where food-size is least variable. Since the timing of the second trial depends on which station was chosen on previous trials and on what the outcomes were, then food will also be obtained at different times. For an animal which always chooses the constant patch, then, after getting two bits of food in trial 2, its position in food-time space is given by C2. An animal that always chooses the variable station, will find itself in one of four possible positions upon receiving its food reward in trial 2 (points V2a, b, c and d). It was shown in section 1) that the constant patch should be preferred while $p/q > Y/T$, where p^2 = variance of food obtained and q^2 = variance of delay experienced in the variable patch, Y = amount of food to be obtained in time T. It can be seen from the example shown in Fig. 7a that the variance of food obtained in the variable patch is the same as that of the delay, whereas $Y/T < 1$. Therefore the the model correctly predicts Caraco's result that birds should prefer the constant patch while feeding rate exceeds energy budget.

Figure 7b shows what we should expect when an animal cannot meet its energy budget. In this case, extrapolating the animal's current rate of feeding to obtain a new goal point will result in the energy budget being met too late or not at all. For an animal which must obtain a certain amount of food by a certain time there will be a maximum time horizon (the end of the day, for example) and a minimum rate of feeding necessary to achieve its goal. Since, in the example shown, variance in food/ variance in delay, is less than Y/T, then the variable station will be preferred.

4.b. "Round-the-clock" foragers -- EH Model-III

So far, the model has been concerned with risk proneness or aversion among animals such as birds which need to build up enough food reserves during the day to last them through the night. Other animals, such as shrews, may feed both day and night, and are not constrained by a

particular deadline. This has implications for their preference or otherwise for variable food sources (Houston and McNamara, 1985). When round-the-clock foragers feed in relatively rich patches, the average feeding rate may be extrapolated to meet the budget line giving a future goal point. The animal need only feed at its current average in order to achieve the goal point and energy balance. In rich patches therefore, round-the-clock foragers should, according to the model, behave like time-constrained foragers. Unlike time-constrained animals, round-the-clock foragers do not, theoretically, need to achieve balance by any specific time. Suppose, for example, an animal is feeding below its budget line but a rate parallel to it: it will never be able to make up its energy debt. On the other hand, the size of the debt will not increase and hence the animal will be no worse off 24 hours later than one hour later. (Of course, being in debt is inherently dangerous, in that an animal with low energy reserves is less likely to survive interruptions in feeding (Barnard et al., 1985).)

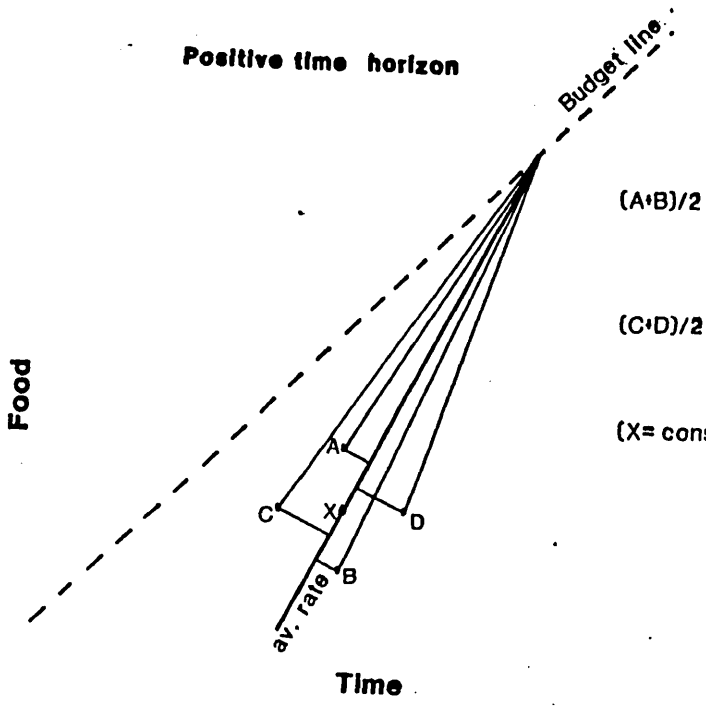
For a round-the-clock forager feeding at a rate less than that required by its budget line, extrapolating the average feeding rate gives an intercept point which lies in the past (Fig. 8b). In this case, the quantity referred to as "expected hunger" might more correctly be called "experienced hunger". Furthermore, under a negative time horizon, the model's predictions of preference or otherwise for variability are the opposite of predictions under a positive time horizon: *hunger is now minimised by choosing the variable patch when food size is manipulated, and by choosing the constant patch when delay is manipulated.*

In summary, the expected hunger model-III predicts that time-constrained foragers should always prefer variability in food delay and always avoid variability in food size. The preferences of round-the-clock foragers should depend on whether or not they can expect to meet their energy budgets. When feeding at a rate greater than that required by the budget line, preferences should coincide with those of time-constrained foragers; when feeding at less than the necessary rate, variability in food delay should be avoided and variability in food size preferred.

Evidence from Barnard and Brown (1985) on risk-sensitive foraging in common shrews (*Sorex araneus*) provides some support for model-III. Shrews, which may feed throughout the day and night, were given the choice of feeding at either a constant food station giving 1 food unit on each

Fig. 8

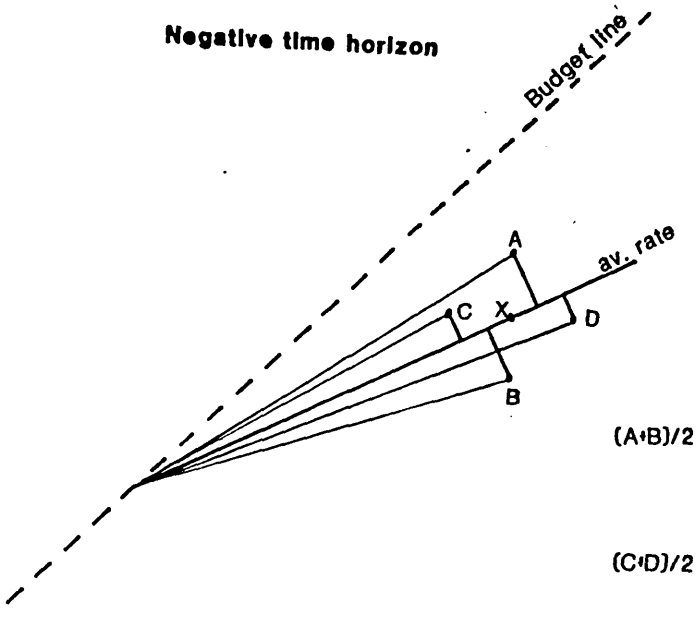
Model III. Risk sensitivity of "round-the-clock" foragers, who do not need to balance energy budgets by a particular critical time.
a) When average feeding rate is sufficient to balance the energy budget, extrapolation results in a positive time horizon and predictions concerning risk sensitivity are the same as those for time-constrained animals. When delay is manipulated, the variable station is preferred. When reward size is manipulated, the constant station is preferred.
b) When average feeding rate is insufficient to meet energy requirements, extrapolation results in a negative time horizon and preferences are reversed. When delay is manipulated, the constant station is preferred. When reward size is manipulated, the variable station is preferred.



(A+B)/2 < X choose constant

(C+D)/2 > X choose variable

(X= constant= 0)



(A+B)/2 > X choose variable

(C+D)/2 < X choose constant

trial or a variable feeding station giving 3 food units on one in three trials and nothing on the other two trials. The timing of trials wasarranged to produce a feeding rate which was either higher or lower than that demanded by the energy budget. (Unlike Caraco's experiments, this delay was not proportional to the amount of food received on the preceding trial.) As predicted by expected hunger model-III, Barnard and Brown found that shrews preferred the variable station when running below budget and preferred the constant station when feeding at higher than the budget rate. It remains to be seen whether, as model-III predicts, these preferences are reversed when food delay rather than food size is manipulated.

4.c. Mean and variance trade-off effects

On functional grounds, optimal foraging theory argues that animals should choose to feed in patches which provide the highest mean reward rate, and that where all means are equal then the variance of feeding rate must be taken into account. The situation when patches differ in both means and variances of feeding rates is more complicated.

Different authors have proposed different models of an animal's preference for mean-variance combinations. Real (1981) suggests that animals will always avoid risk and attempt to maximise mean rate of food intake (μ) discounted by some constant (k) proportion of its variance (σ^2), i.e. they should maximise some function (F),

$$F = \mu - k.\sigma^2$$

Stephens and Charnov (1982), on the other hand, propose that animals should minimize some function (z),

$$z = (R - \mu)/\sigma$$

where R is the feeding rate necessary if the animal is to survive the night. Caraco and Lima (1985) and Stephens and Paton (1986) note that the z-score model, unlike the variance discounting model, does not predict constant risk aversion. The z-score model predicts that as the mean food gain increases generally, animals should be increasingly ready to forego some food gain in order to enjoy a reduced variance. Stephens and Paton (1986) carried out an experiment to distinguish between the two models. They presented hummingbirds (*Selaphoruous rufus*) with a choice betwen a large reward with a large variance and small reward with a small variance. Having established the birds' preferences, they increased both means by a

fixed amount, keeping the variances unchanged. The variance discounting model predicts that, regardless of which reward was preferred, individuals should not change that preference in response to the general increase in reward size. The *z*-score model says that animals should increasingly prefer the small mean, small variance alternative: "a relatively high mean may be worth suffering the higher variance when means are generally low, but when means are increased, a lower variance becomes more important than a relatively high mean." The authors did indeed find that preference for the high mean, high variance alternative, decreased with increasing reward size. The EH model-II (and III) makes a similar prediction. Figure 9, using the relative reward sizes adopted by Stephens and Paton, shows that animals should always prefer the larger sized, larger variance reward but that this preference should decrease linearly as both rewards increase in size. This may be expressed mathematically as follows. Let the difference in H between a patch providing a high mean, high variance reward ($\mu_{high} \pm \sigma_{high}$) and a low mean, low variance reward ($\mu_{low} \pm \sigma_{low}$) be expressed as $H_{high} - H_{low}$. If both means are increased by a constant value x, then, from equation (2.2), the increase in H for the high mean reward is given by,

$$H_{high+x} - H_{high} = \frac{x.(TY^2 - TY.(\mu_{high} + \sigma_{high}) + T^3)}{2.(T^2 + Y^2)}$$

and for the low reward,

$$H_{low+x} - H_{low} = \frac{x.(TY^2 - TY.(\mu_{low} + \sigma_{low}) + T^3)}{2.(T^2 + Y^2)}$$

where T and Y are constants representing total time available and total food to be obtained. The effect on H, of an increase of mean (x) is less pronounced on the high mean than on the low mean reward. Thus, the difference

$$(H_{high+x} - H_{high}) - (H_{low+x} - H_{low}) = \frac{xTY.[(\mu_{low} \pm \sigma_{low}) - (\mu_{high} \pm \sigma_{high})]}{2.(T^2 + Y^2)}$$

is always a negative value. In other words, the effect of increasing the means by a constant value is to reduce the difference (in H) between them.

Barnard, Brown, Houston and McNamara (1985) develop a model for shrews, which makes the following predictions, for individuals feeding at less than the necessary rate. 1) When the mean feeding rate at the variable station is greater than that at the constant station, shrews should prefer to forage at the variable station, but this preference should wane as variance increases. 2) When the mean feeding rate at the variable station is lower than that at the constant station, shrews should prefer

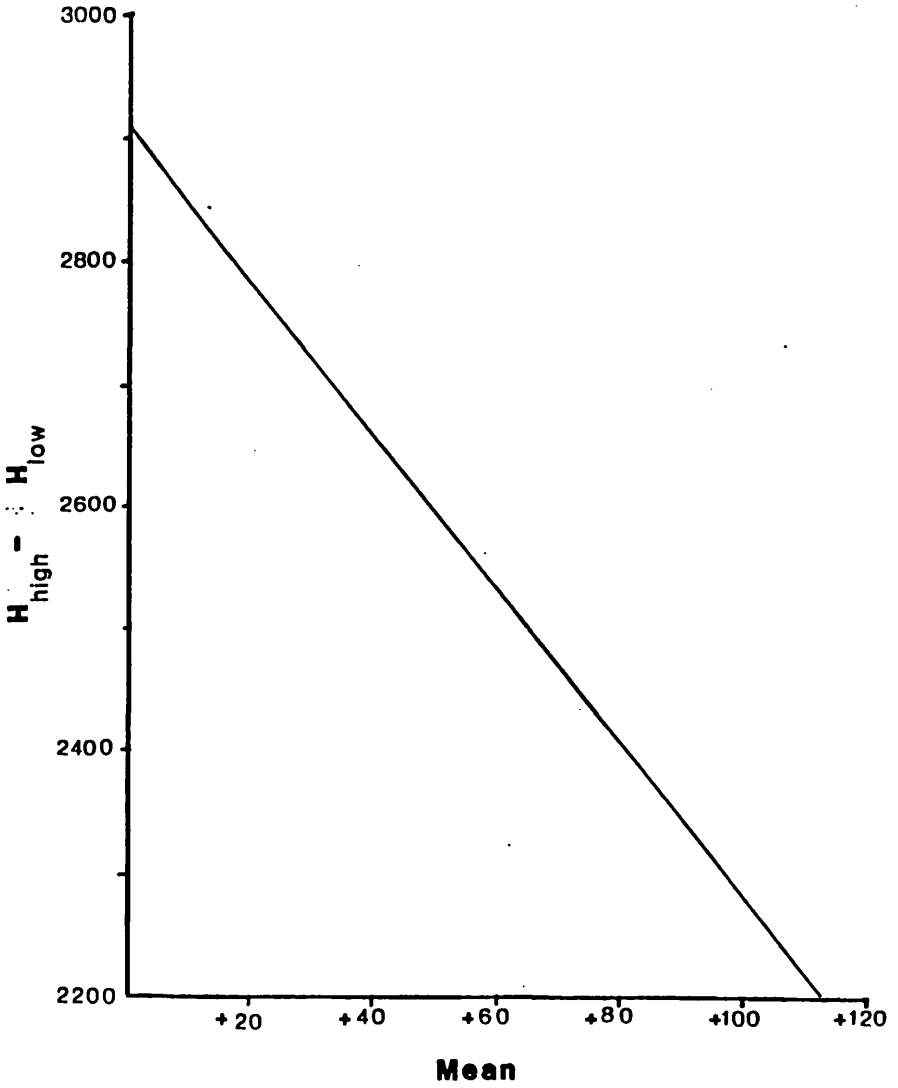


Fig. 9

The x-axis shows the relative advantage (in terms of H) in choosing a high mean, high variance reward over a low mean, low variance reward. As the means of both rewards are increased (leaving the variances unchanged), the advantage in choosing the large reward decreases. At the origin, the mean of the low reward is 12.5 ±2.5, while the mean of the high reward is 25 ±15. Both means are increased by 20 for each division of the y axis. (Y=T=500, see text.)

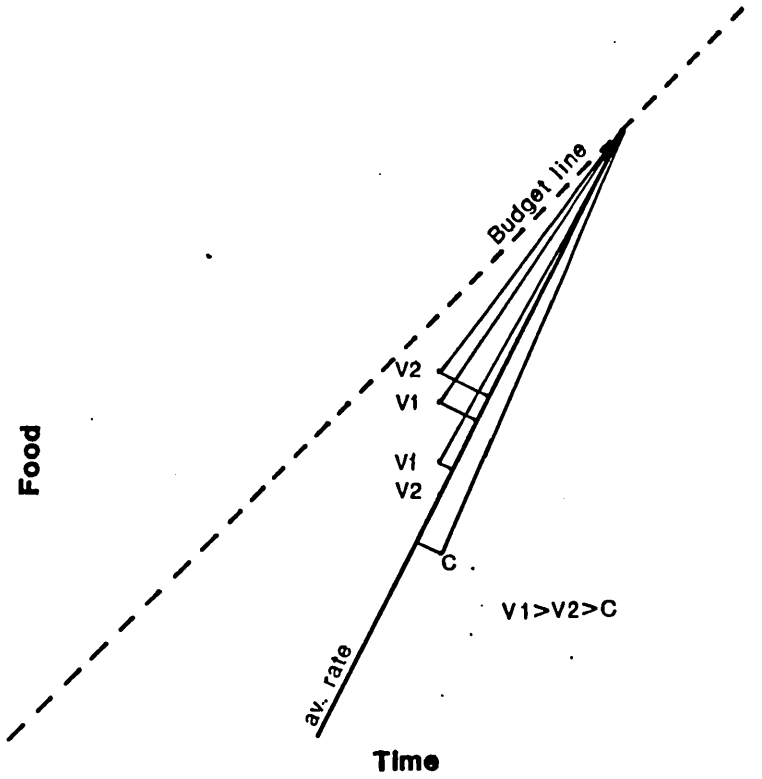
the constant station, but this preference should wane as the variance at the variable station increases. The results of an experimental test ofthese predictions were equivocal. Shrews, through a series of 30 forced trials, were trained to expect a single food unit per visit to the constant station and one of seven mean/variance combinations at the variable station. The mean reward rate at the variable station was either 0.67, 1, or 1.33 food units per visit. Animals experienced two variance levels with each of the first two means and three variance levels with the third mean. When animals were free to choose between stations, Barnard et al found that the precise degree of variance experienced during training had no clear effect on preference. When however, the variance experienced *during* preference tests was examined and correlated with the preference shown, the initial predictions were found to be upheld.

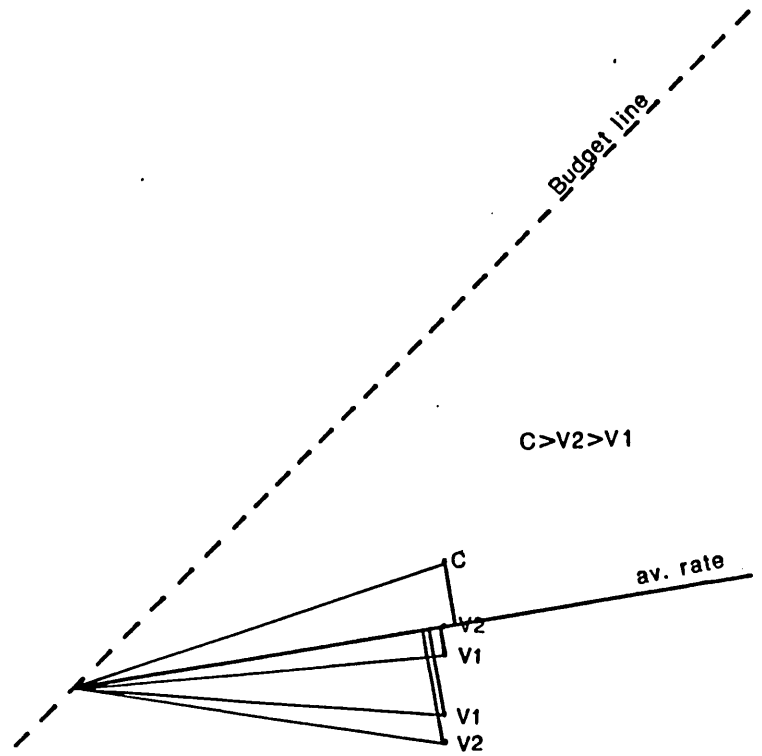
It should be noted however that the experimental conditions under which preferences were tested, were somewhat different to the training conditions. During training animals were occasionally denied access to the food stations to ensure that the overall feeding rate did not exceed 2/3 the rate required to meet daily budgets. In the preference tests this restriction was relaxed; preference tests were run for 20 trials or 2.5 hours, whichever came first. Barnard and Brown (1985), found that shrews required between 6.5 to 12.4 mealworm segments per hour. Thus, assuming 20 trials run in 2.5 h, individuals may have been receiving 5.36 segments/h (for variable patches with a mean of 0.67), 8 seg./h (for patches with a mean of 1) or 10.64 seg./h (for means of 1.33). It is therefore possible, especially when receiving a mean of 1.33 food units per visit, that shrews were feeding *above* their necessary feeding rates, in which case the above predictions would probably be invalid.

If, during preference tests, shrews feeding in variable patches with high means were feeding above their necessary feeding rates, while those feeding in low-mean patches were failing to meet energy budgets, then the expected hunger model-III makes the same predictions as Barnard et al.'s functional model. In Figure 10a, where the mean reward rate at the variable patch is 1.33 seg./visit and that at the constant patch is 1 seg./visit, we assume that the average feeding rate is greater than the necessary rate. Expected hunger is less in the variable patch, and so this patch should be preferred. However, since the time horizon is positive, variance in food size should be avoided. Therefore, the variable station should be preferred rather than the constant station but this preference should wane as

Fig. 10

Mean/variance trade-off effects for a "round-the-clock" forager.
a) When the time horizon is positive, the variable station (V_1) should be preferred if it offers a higher feeding rate than the constant station (C). But as the variance increases (V_2), that preference should decrease.
b) When the time horizon is negative, the constant station should be preferred if it offers a higher feeding rate than the variable station. But that preference should decrease as the variance of the variable station increases.


Budget line
Food
V2
V1
V1
V2
C
V1>V2>C
av. rate
Time


Budget line
C>V2>V1
C
av. rate
V2
V1
V1
V2

variance increases. When the mean reward rate at the variable station is 0.67 seg./visit and that at the constant patch is 1 seg./visit (see Fig.10b), we assume that the average feeding rate is less than the necessary rate. Hunger is less in the constant patch and so this patch should be preferred. However, since the time horizon is negative, variance in food size should be attractive. Therefore the constant patch should be preferred but this preference should wane as the variance of the variable patch increases.

5. "BIRD-IN-HAND" EXPERIMENTS

5.a. Preference for short-term benefits.

Birds do not always forage efficiently. One well documented instance of their less than optimal foraging behaviour is their tendency to choose an immediate small food reward in preference to waiting a little longer for a much larger reward. The phenomenon was first investigated by Rachlin and Green (1972), and similar results have obtained by Ainslie (1974), Mazur and Logue (1978), Lea (1979), Green et al. (1981) and others. An interesting feature of the phenomenon is that the longer the delay before a reward is obtained, the more likely that birds will choose to forego the smaller reward and wait for the larger one. For example, a pigeon given the choice of an immediate reward of 2 sec access to a grain hopper and a reward of 4 sec access for which it must wait a further 4 sec, will invariably choose the immediate 2 sec reward. When, however, the pigeon is asked to choose between a 2 sec reward preceded by a 16 sec wait or a 4 sec reward preceded by a 20 sec wait, the bird is more likely to choose the 4 sec reward (Rachlin and Green, 1972). It acts as if "a bird in the hand is worth two in the bush," (while recognising that two birds in the bush are still worth more than one bird in the bush).

Recently, Kagel, Green and Caraco (1986) have proposed a model, derived from economic theory, to describe this result (see also Stephens et al., 1986, for a model based on the marginal value theorem, and Fantino and Abarca, 1985). An animal discounts the value of a promised reward in proportion to the delay before the promise is fulfilled. In particular, the model assumes a variable time bias, in which the present value of a future reward is discounted at a rate which itself is a function of time. The authors propose that the present value (PV) of a reward of size c which will be forthcoming in t secs may be modelled as

$$PV(c,\ t) = c.\exp\left[- \int_0^t \lambda(t).dt \right] \qquad (5.1)$$

where $\lambda(t) > 0$ is the instantaneous discount rate and is a function of time. In the standard economic model, the time bias is assumed to be constant, so that $\lambda(t) = \lambda$ and (5.1) reduces to

$$PV(c, t) = c.e^{-\lambda t} \quad (5.2)$$

Given two rewards of different sizes, due at different times, the use of a constant time bias in (5.2) will result in a consistent bias towards one of the rewards. For example, with $\lambda = 0.5$, Figure 11a shows how the worth of two rewards whose immediate values are 2 and 6, dwindles with time. It may be seen that an immediate reward of 2 units is worth more than 6 unit reward 3 sec later, and that the smaller reward will always be worth more than the larger reward delayed by an additional 3 sec. In Figure 11b the same example is repeated using a variable time bias. (In this case $\lambda(t) = e^{-0.5t}$.) Again, an immediate reward of 2 units outweighs a 6 unit reward at 3 sec. However, as the rewards are postponed further into the future, the larger, more delayed reward becomes the more valuable option. In general, Kagel et al. show that foragers may show such reversals of preference providing that $d\lambda(t)/dt < 0$. Interestingly, the expectation of time-dependent preference reversals is an integral feature of the expected hunger model-II. Fig. 11c describes how expected hunger increases (H becomes smaller) with reward delay for rewards of 2 and 6 units separated by a 4 sec delay.

Figure 12, shows in more detail how the expected hunger model-II may be used to explain the findings of Green et al. (1981). In this experiment, four pigeons, in an operant conditioning apparatus could choose to have a small reward preceded by a small delay or a larger reward preceded by a larger delay. Each trial lasted 40 sec (see Fig. 12c) and could be divided into 5 stages; a search time of t_s sec was followed by the chance to choose between a "short" prey or a "long" prey; having chosen, there followed a handling time of t_h sec which was shorter for the "short" prey than the "long" prey, and a feeding time of t_f sec access to a grain hopper which, again was shorter for the "short" prey; finally, if the short prey was chosen, there followed t_n sec of non-foraging time, before the next trial began. The short prey, consisting of 2 sec feeding time, was always obtained 30 sec into the trial and was followed by 8 sec non-foraging time. The long prey was always obtained 34 sec into a trial and consisted of 6 sec access to the grain hopper, after wich the next trial began. The experiment consisted of varying the time at which the birds could choose between the two alternatives, by varying the length of the search time from 2 to 28 sec. As with Rachlin and Green (1972), it was found that the longer the handling time t_h (and hence the shorter the search time t_s) the more often the birds chose the long prey. In each of

Fig. 11

a) and b) Effect of constant and variable discounting rates on the present value of a food item. Both figures show that the present value of a food item declines the longer the time the food takes to arrive.

$$PV(c, t) = c.\exp[-\int_{o}^{t} \lambda(t).dt]$$

Where PV(c, t) is the present value of an item of c units, at time t, and $\lambda(t)$ is the instantaneous discount rate. In both figures, immediate access to a food item worth two units is preferred to six units delayed by three seconds. However, in figure a) the instantaneous discount rate is constant (at 0.5) which ensures that the smaller reward will always be preferred to the larger reward, as long as it arrives 3 sec earlier. In figure b) λ is itself dependent on t, and as both rewards are increasingly delayed, preference for the more immediate smaller one, changes to preference for the more delayed, larger one. c) The expected hunger model-II makes the same predictions as the variable time bias discount model (Fig. b). That is, immediate access to a small reward may result in a greater H value than delayed access to a larger reward. However, as both rewards become increasingly delayed, H for the smaller reward may fall below that for the larger one, and preferences should be reversed.

Fig. 11a

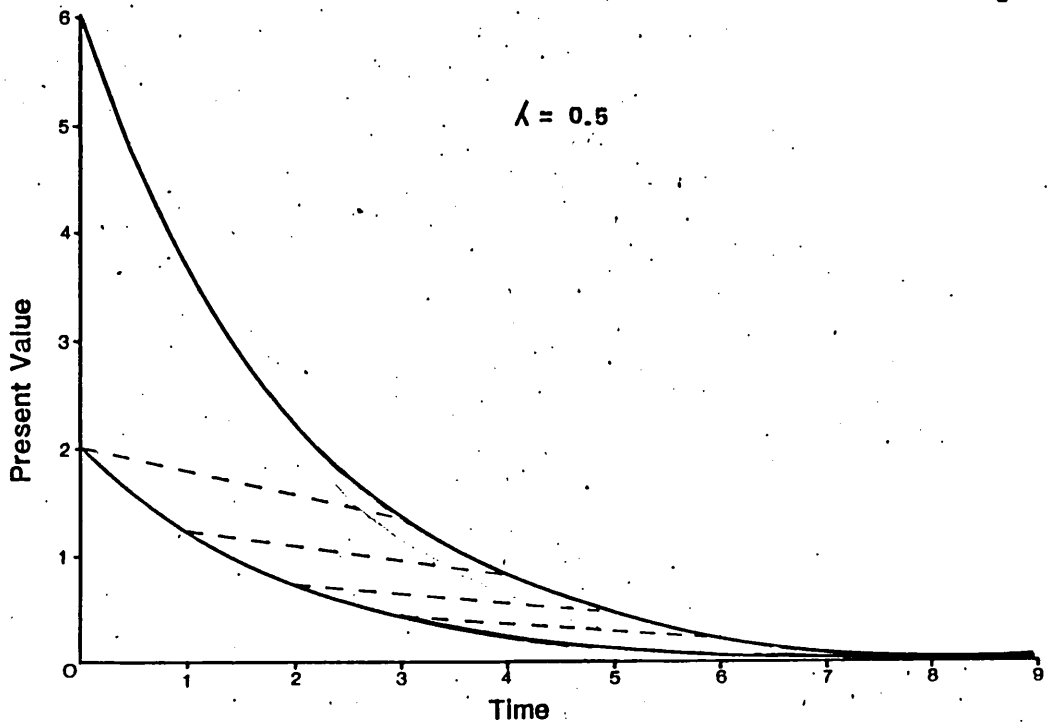


Fig. 11b

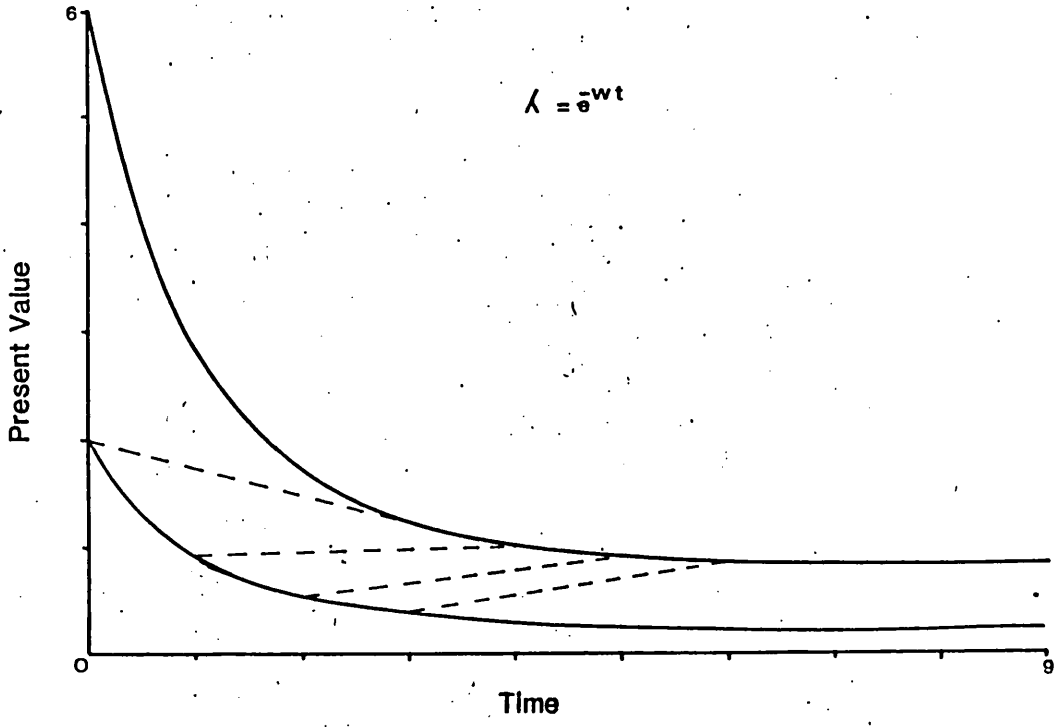
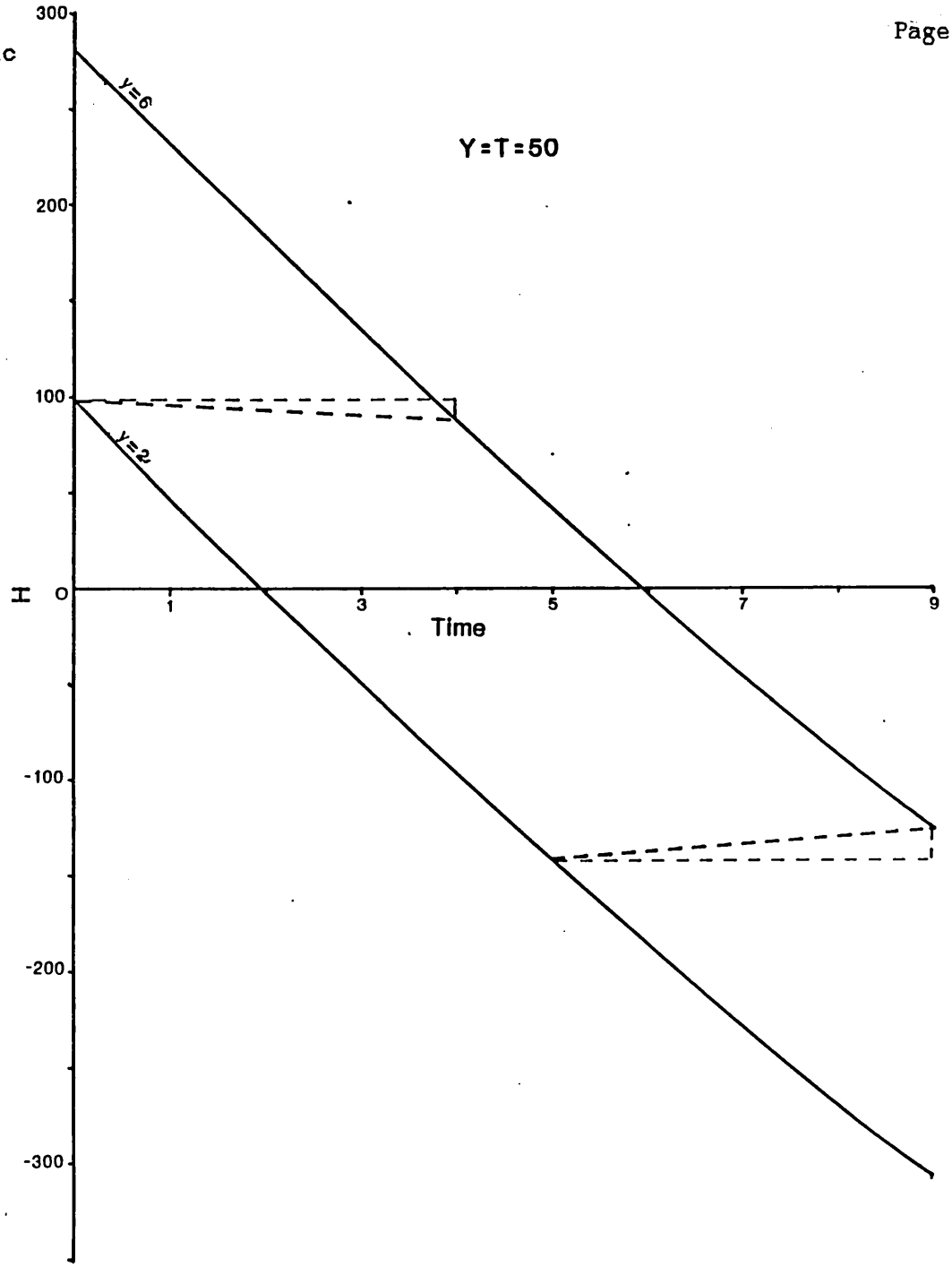


Fig. 11c

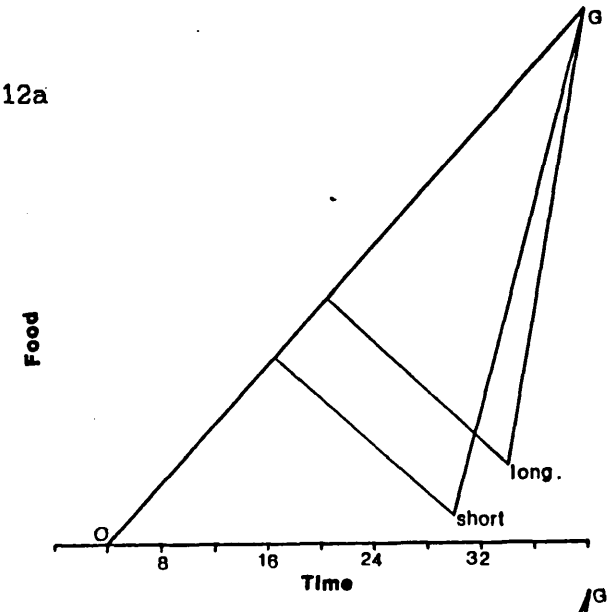


the four birds tested, clear preferences for the short prey, were gradually weakened and reversed, becoming clear preferences for the long prey, as handling times were lengthened.

Throughout the experiment, all birds were chronically food deprived, being maintained at 80% of their normal bodyweights. We may assume therefore, that feeding rates during the trials fell short of the necessary budget. At the point where birds must choose the long or short prey, the minumum necessary feeding rate required to satisfy the energy budget is given by the line OG (see Fig. 12a). As the search time (t_s) becomes longer and the delay between choosing and obtaining a prey (t_h) becomes shorter, the minimum necessary feeding rate becomes steeper (Fig. 12b). Figure 13 shows the relationship between the difference in expected hunger (H for long prey minus H for short prey) and the handling time for the short prey, using different goal points G (with coordinates Y,T). Since H is negative for both prey types, a positive difference indicates that the long prey entails less expected hunger and should be preferred; negative values suggest that the short prey should be preferred. All of the curves suggest that preference for the long prey should increase with pursuit time.

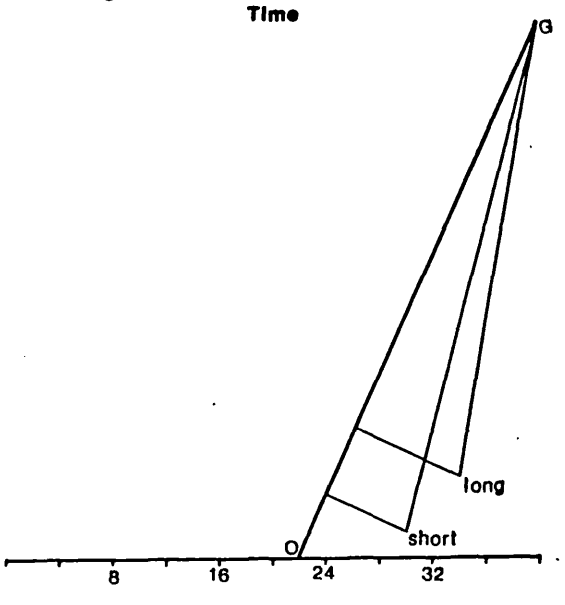
Furthermore, for a given time horizon (T), the preference for the short prey becomes less marked as the food goal (Y) is lowered. For example, with a time horizon of 40 sec and a food goal of 50 units, the short prey should be preferred at all t_hs less than 16 sec; with food goals of 40 and 30 units, short prey should be preferred at t_hs less than 12 and 8 sec, respectively. Thus the hungrier the bird, the stronger its tendency to opt for small, less delayed rewards in preference to larger, more delayed rewards. Evidence in support of this prediction comes from Snyderman (1983), Abarca et al (1985) and Rechten et al. (1983). Snyderman presented pigeons with a foraging schedule in which "short" and "long" prey were encountered sequentially. As in the experiments already described, "long" prey were larger but more delayed than "short" prey. Snyderman found that when pigeons were maintained at 95% normal bodyweight they rejected more "short" prey than they did when maintained at 80% bodyweight. Similarly, in an experiment in which long and short prey were the same size, Abarca, Fantino and Ito (1985) found that pigeons maintained on a closed economy (where all food was obtained in the experimental apparatus and the birds gained weight during the experiment) were more likely to accept a long prey when offered than were birds

Fig. 12a



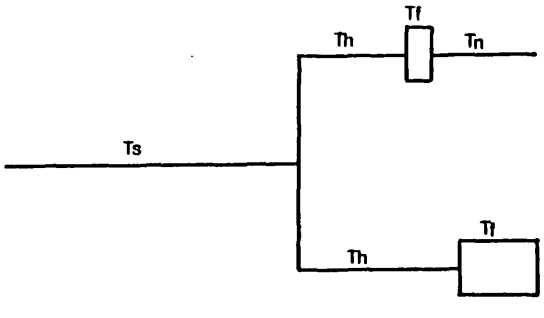
$H_l > H_s$ choose long

Fig. 12b



$H_l < H_s$ choose short

Fig. 12c



Preference for a large delayed reward (a) changes to preference for a smaller less delayed reward (b) as both rewards become imminent. In Fig. 12c, T_s = search time, T_h = handling time, T_f = time spent feeding, T_n = non-foraging time.

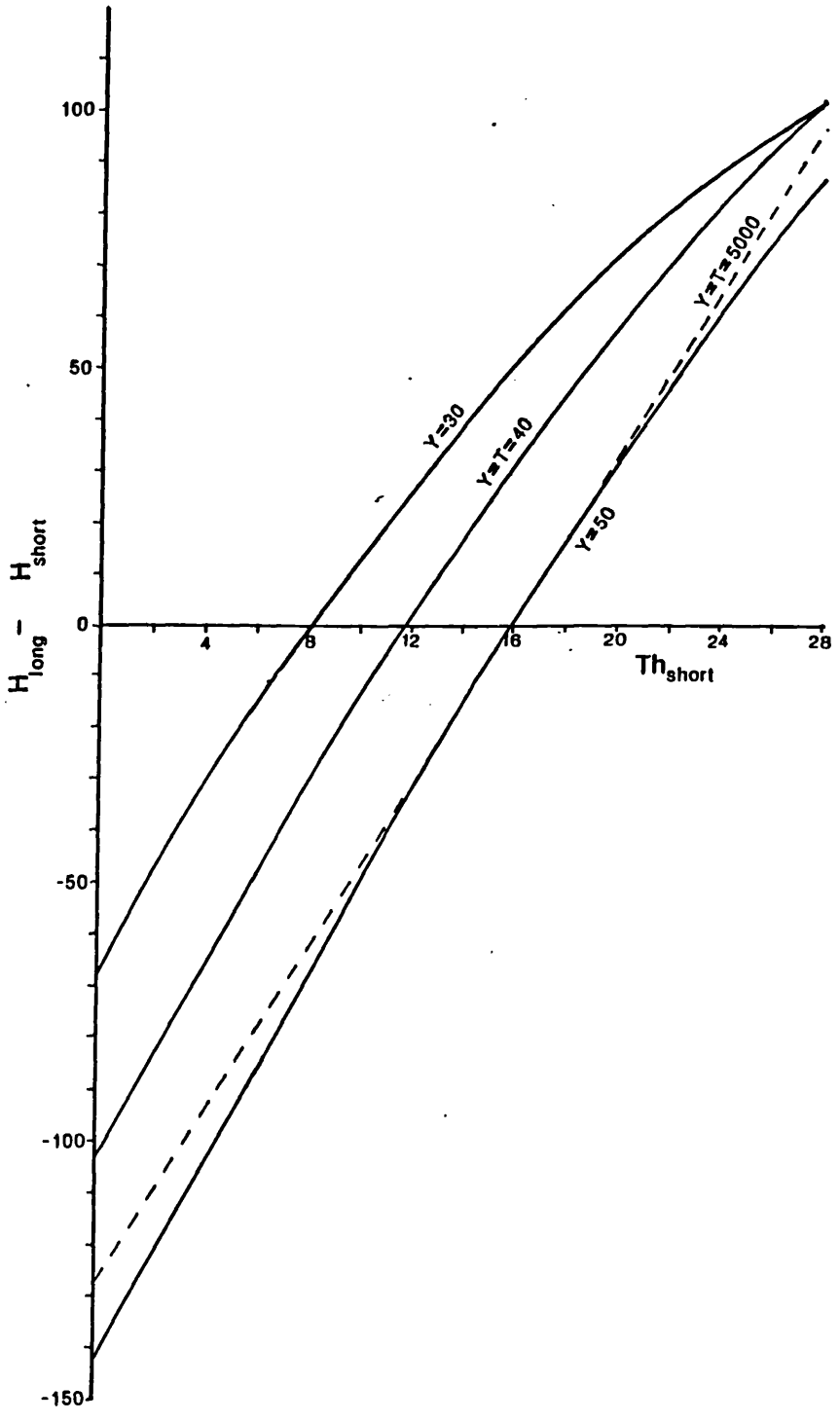


Fig. 13
Change in difference in H (between choosing the long and short food item in Fig. 12) as handling time increases. As handling time increaes, preference for the short item ($H_{long} - H_{short} < 0$) changes to a preference for the longer item ($H_{long} - H_{short} > 0$). For a given time horizon (T=40), then the greater the food deficit (Y), the stronger the preference for the more immediate smaller reward.

maintained on an open economy (kept below 80% bodyweight, and fed in the home cage as well as the experimental apparatus). In an experiment with great tits, Rechten et al. found that hungry birds presented with food items on a moving conveyor belt were less able than better-fed birds to pass over small food items and to wait for large items to appears.

An animal's degree of hunger has been shown to affect its foraging decisions in species other than birds. Ebersole and Wilson (1980) allowed deermice (*Peromyscus leucopus*) to forage for five different types of seed buried in sand. Six levels of food deprivation were imposed and the authors found that the hungrier the deermice, the more seed types they included in their diet. Ebersole and Wilson suggest that the animals were using hunger level to gauge food density, and optimal foraging theory predicts that as the density of preferred food items falls, then other less-preferred items should be included. (Lacher et al. (1982) come to a similar conclusion from a study of guinea-pigs foraging for different varieties of leaves). In another experiment, Ebersole and Wilson increased the seeds' handling times by wrapping them in rubber bands. Deermice now became much more selective about the seeds they ate. This result agrees with the observations above, that increasing prey handling times leads to an increasing rejection of less-profitable prey.

Among insects, Molles and Pietruszka (1983) found that "satiated" stoneflies (*Hesperoperla pacifica* (Banks) and *Megarcys signata* (Hagen)), feeding on mayflies, were more likely to attack their preferred prey species (*Baetis tricaudatus* Dodds), whereas fasted stoneflies attacked preferred and less-preferred species (*Ephemerella altana* Allen) with equal frequency. In an experiment by Stephens et al. (1986), honeybees (*Apis mellifera ligustica*) were more likely to pass over a weak-nectar flower to forage at a more profitable but more distant flower, when the habitat as a whole was rich rather than poor. Charnov (1976) describing the attack strategy in the mantid (*Hierodula crassa*) noted that the longer the animal had gone without food, the more likely it was to stalk houseflies that were out of reach. Again, Charnov assumes that being hungry is a sign to the mantid that its preferred prey (houseflies *within* striking distance) are scarce.

It would seem likely that in each of these examples, regardless of the actual encounter rates, animals use the degree of hunger they are feeling as a guide to the abundance of their favoured food items. That animals

appear to use hunger as a proximate cue in deciding how to forage, fits in well with the expected hunger model.

5.b. Preference for variance in sequential encounters

In an experiment by Lea (1979), pigeons "foraging" in a Skinner box encountered two prey types -- a "long" prey obtained after 20 sec and a "short" prey of the same size obtained after 5 sec handling time. On encountering a given prey, pigeons could choose to accept it and endure the handling time associated with it, or reject it and search for another prey. In Lea's experiment, there were equal numbers of "long" and "short" prey and, for a given foraging session, the search time was fixed. Under these conditions, pigeons can get the most food in the quickest time by always accepting a short prey when one is found. Whether a long prey is accepted should depend on the length of the search time between prey; the longer the search time, the greater the benefit in accepting the long prey. Theoretically, preferences should be all or nothing; when the search time is longer than 7.5 sec, the long prey should always be accepted, and it should always be rejected when search times are less than this. Lea found that pigeons were more inclined to accept the long prey when the search time was also long, but this preference changed gradually, rather than suddenly, as the search time was shortened. Furthermore, pigeons rejected the long prey more often than they should have done (assuming that they wished to maximise food intake). When the search time was 7.5 sec pigeons showed a strong tendency to reject the long prey, whereas optimal foraging theory predicts that the long prey should be accepted or rejected on an equal number of occasions.

As Lea points out, the preference for rejecting long prey and opting to search, is consistent with the bias towards variable interval (VI) over fixed interval (FI) schedules of reinforcement found in operant conditioning studies (eg. Herrnstein, 1964; Davison, 1969). When the search time is 7.5 sec, pigeons must choose between accepting a certain reward in 20 sec time, or choosing to search and receive, with equal probability, a reward in 12.5 sec or 27.5 sec. Energetically, there is no difference between the options, but if expected hunger is to be minimised (see section 1), the certain long prey should be rejected in favour of the variable option.

Abarca and Fantino (1982) repeated Lea's study with some slight changes. They suggested that the birds' bias towards searching for short prey (rather than accepting long prey) may be an artefact, arising from Lea's use of fixed intervals for the prey "handling times". The authors used variable intervals for the handling times, since "it was expected that the use of VI schedules might produce results more compatible with optimality theory", though they gave no theoretical reason for expecting this. Their results, in contrast to Lea's, showed that when the search time was FI 7.5 sec (and handling times were VI 20 and 5 s) then the pigeons' behaviour was optimal -- they accepted or rejected the long prey with equal likelihood. Abarca and Fantino's experiment suggests that choice behaviour will be more optimal when VI, rather than FI, schedules are used for handling times. The expected hunger model makes a similar prediction.

In Lea's experiment search times and handling times take the form of FI schedules. The difference in expected hunger between accepting or rejecting the long prey may be expressed as,

$$Diff_{acc-rej} = H_l - \frac{(H_{l+sch} + H_{s+sch})}{2} \qquad (5.3)$$

where sch = search time, l = handling time for long prey, and s = handling time for short prey. According to optimal foraging theory the energy difference between accepting and rejecting the long prey should be zero when,

$$sch = \frac{l - s}{2} \qquad (5.4)$$

Substituting (5.4) into (5.3) gives,

$$Diff_{acc-rej} = H_l - \frac{(H_{s\ l-s} + H_{l+s})}{4} \qquad (5.5)$$

From section 1, the expected hunger at time (t) and with food eaten (y) is,

$$H_{t,y} = \frac{(y.T - t.Y).(Y^2 - y.Y + T^2 - t.T)}{2.(T^2 + Y^2)}$$

Since, in these experiments, the size of the food reward (y) is the same regardless of the bird's choice, its absolute value is irrelevant to the decision process and this equation may be simplified by setting (y) to zero, i.e.,

$$H_t = \frac{T.Y.t^2}{2.(T^2 + Y^2)} - \frac{t.Y}{2} \qquad (5.6)$$

Substituting (5.6), with the appropriate values of (t), into (5.5) and rearranging gives

$$Diff_{acc-rej} = -(1-s)^2 . \frac{T.Y}{8.(T^2+Y^2)} \quad (5.7)$$

This is identical to equation (2.4) in section 1 of this chapter describing the cost of choosing the constant station (relative to the variable station) when the delay of a food reward is varied.

In Abarca and Fantino's (1982) experiment, the average handling times for long and short prey were the same as in Lea (1979) but they were variable rather than fixed. The simplest way to model this variation is to assume that for each prey type there are two equiprobable handling times, symmetrical about the mean. Thus, the handling time for the long prey is 1 ± p, and that for the short prey is s ± q. When a bird "finds" a long prey, it may choose to accept it, in which case it will finish handling it in either 1+p or 1-p sec; or reject it and continue to search, in which case it will obtain its prey after a delay of either sch+s+q, sch+s-q, sch+1+p or sch+1-p sec. When the search time (sch) is (1-s)/2, the energetic costs of accepting or rejecting the long prey are identical. The costs, in terms of expected hunger may be calculated as before by substituting the appropriate values of (t) into (5.6) giving,

$$Diff_{acc-rej} = (2.(p^2-q^2) - (1-s)^2) . \frac{T.Y}{8.(T^2+Y^2)} \quad (5.8)$$

Given that T and Y are positive, the difference in equation (5.7) will always be negative and therefore birds will tend, "wrongly", to reject long prey when handling times are fixed. Whether equation (5.8) is negative, depends on the relationship between handling time variances of the short and long prey. If the variance (p^2) of the long prey is greater than the variance (q^2) of the short prey, then the difference in equation (5.8) will be less negative than that in equation (5.7) and the tendency to reject long prey will be less pronounced when handling times follow a VI schedule than when they follow an FI schedule. Abarca and Fantino give no details of the degree of variance programmed into their VI schedules but most mechanisms commonly used in operant conditioning experiments generate variances which are proportional (and perhaps) equal to the mean interval (Lea, personal communication). It is therefore highly likely that p was greater than q in Abarco and Fantino's experiment and, accordingly, that the expected hunger model-II correctly predicts their results. In Figure 14a, handling time and search time values are as for Abarco and Fantino, and the variance is set equal to the mean interval (ie $p^2 = 1$ and $q^2 = s$). It may be seen that there is a bias towards rejecting long prey

(all lines are to the right of the optimum at 7.5 sec) but that this is consistently less pronounced for VI handling times than for FI handling times. When the handling time variances are set equal to the mean squared (ie $p^2 = l^2$ and $q^2 = s^2$) then the difference between the two schedules is further exaggerated to the extent that VI handling times should produce a bias towards accepting the long prey (Fig. 14b).

Abarca and Fantino extended their experiment by varying search times as well as handling times. As in the previous experiment, birds rejected long prey less frequently as the search time was increased. Similarly, the change with search time from rejecting to accepting the long prey occurred close (at about 5 sec) to the optimum (7.5 sec). Predictions of the expected hunger model-II can be derived for the simplest case, where there are only two equiprobable search times (sch ± z sec). A bird "finding" a long prey can choose to accept it and endure l+p or l-s sec; or it may reject it and search for another prey which it may obtain after one of 8 possible intervals have elapsed -- sch+z+s+q, sch-z+s+q, sch+z+s-q, sch-z+s-q, sch+z+l+p, sch-z+l+p, sch+z+l-p or sch-z+l-p sec. When sch = (l-s)/2, the difference in expected hunger between accepting and rejecting the long prey can be expressed as,

$$\mathrm{Diff}_{acc-rej} = (2.(p^2-q^2) - (1-s)^2 - 4.z^2) \cdot \frac{T.Y}{8.(T^2+Y^2)} \qquad (5.9)$$

Comparing (5.9) with equations (5.7) and (5.8) (see Figs. 14a and 14b) shows that making both search time and handling time variable should restore some of the bias toward rejecting long prey that was seen when both handling and search time were fixed (Lea's experiment). This is seen most clearly in Fig. 14a (where variance = mean interval), and contrasts somewhat with Abarca and Fantino's finding. The expected hunger model predicts some bias toward rejecting the long prey whereas Abarca and Fantino found a slight bias toward accepting it.

Fig. 14

The tendency to reject a food item with a long handling time in favour of searching for one with a short handling time decreases as search time increases. In each case, the average handling time for a short item is 5 sec, while that for a long item is 20 sec. Animals should be indifferent between searching for a short item or accepting a long item when the search time is 7.5 sec. The expected hunger model-II makes different predictions depending on whether or not handling time and/or search time are fixed or variable, and on the precise relationship between the average delay and its variance.
a) When mean delay (handling time and/or search time) and variance about the mean are equal, then animals will always have a tendency to favour searching for shorter items. This sub-optimal tendency is least pronounced when handling time is fixed and search time is variable.
b) When variance is the square root of the mean, then variable intervals should produce a (sub-optimal) tendency to accept the long prey rather than search for a short prey.

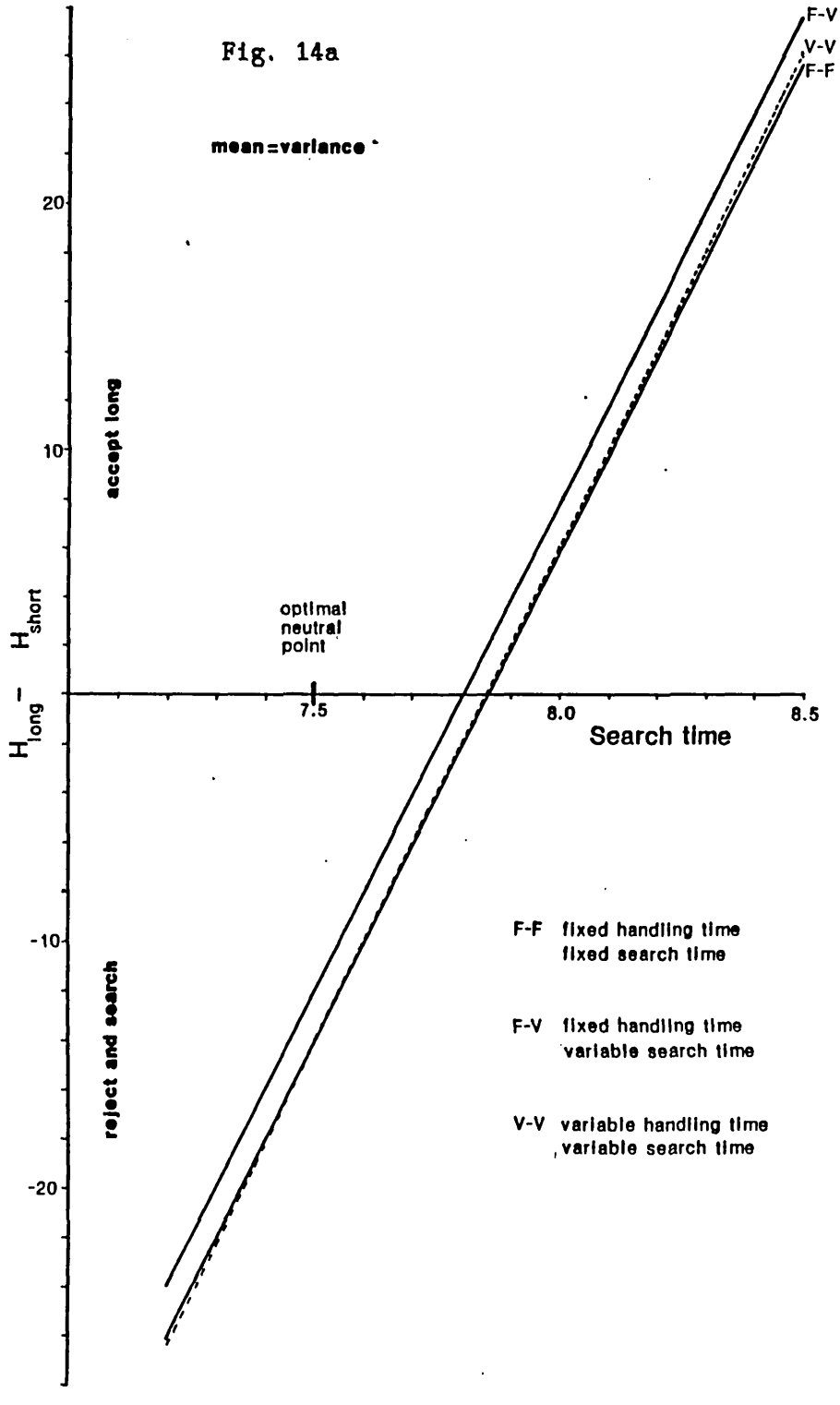
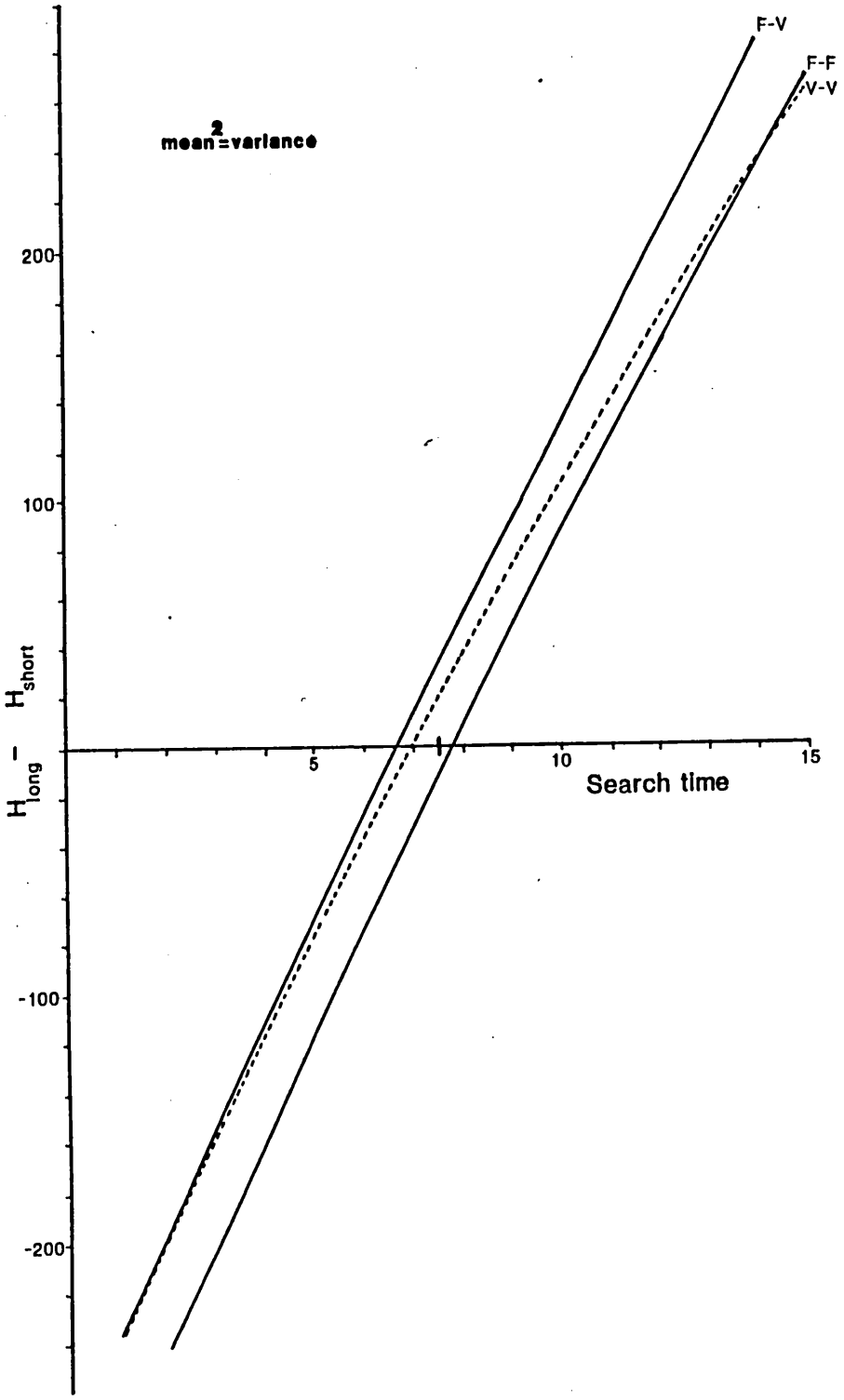

Fig. 14a
mean=variance
F-V
V-V
F-F
20
10
-10
-20
accept long
reject and search
optimal
neutral
point
7.5
8.0
8.5
Search time
H short - H long
F-F fixed handling time
fixed search time
F-V fixed handling time
variable search time
V-V variable handling time
variable search time

Fig. 14b


mean²=variance
F-V
F-F
V-V
200
100
-100
-200
5
10
15
Search time
H_long - H_short

6. SUMMARY AND DISCUSSION

In section 1 and 2 a model (EH-I) was developed to explain why birds, in a series of experiments by Caraco, appeared to follow the expected-energy-budget rule: "Be risk averse if your expected energy budget is positive; be risk prone, if your expected energy budget is negative." There are functional reasons why animals should obey this rule and models have been proposed which predict it (e.g. Real, 1980; Stephens and Charnov, 1982). Nevertheless, it was argued that Caraco had conducted his experiments in a way that failed to prove that his subjects were genuinely sensitive to risk. The expected hunger model-I accommodates Caraco's results and the tendency, noted in the literature, for animals to avoid risk when reward size is varied and to seek risk when the timing of a reward is varied. The expected hunger model is a causal model, and it suggests that risk sensitivity can be explained as a non-functional artefact of a more general foraging mechanism. It also implies that the functional advantages of following the expected energy budget rule are not very great.

In section 3 the model was modified. By allowing the animal's goal point to vary in relation to its average feeding rate, it was shown that the expected hunger model-II performed as a very efficient forager in an environment of depleting patches. It performed well when the patches were of mixed quality, when the travelling time between them was variable, and when the distribution and size of food items within a patch was "stochastic". It was also shown that a model requiring only that the animal monitor its average rate of feeding, performed as well, and often better, than the more complex expected hunger model-II.

Although the expected hunger model explains Caraco's results, it has not been tested directly. Neither have there been many tests of the expected energy budget rule; it would be premature to dismiss it. Experiments by Barnard and Brown (1985) using shrews seem to confirm the expected-energy-budget rule. However, unlike birds, shrews may feed both day and night. There are functional grounds for believing that their sensitivity to risk will differ from time-constrained animals (Houston and McNamara, 1985). In section 4 it was shown that the expected hunger model could be adapted (EH-III) for "round-the-clock" foragers - who have no

fixed end-of-day goal point - and thereby accommodate Baranard and Brown's findings. Its predictions agreed with the findings of Stephens and Paton (1986) showing that, as mean reward increases, hummingbirds are more likely to trade a large reward with a large variance for a smaller reward with a smaller variance. The adapted model-III was also capable of predicting a result of Barnard, Brown, Houston and McNamara (1985) in which it was found that shrews, while generally preferring to feed where food was most abundant, would moderate their preferences according the variance of the alternatives. Again, it should be stressed that in a field where facts are few and poorly established, it is easy to account for them by building unlikely or unproven assumptions into the model. On balance, Barnard and Brown's findings probably strengthen the evidence for an expected-energy-budget rule, rather than that for the expected hunger model. If the expected hunger model is to be preferred over strictly functional models then it must be tested directly. In particular, it should predict the circumstances under which animals will show non-optimal risk sensitivity. The most general testable prediction of the expected hunger model, in all three versions, is that the conditions under which an animal prefers variance in reward size are the conditions under which it avoids variance in reward timing and *vice versa*.

In section 5 model-II was applied to several phenomena from the operant psychology literature, in which animals have repeatedly been shown to make "bad" foraging decisions. For example, it is well established that animals in Skinner boxes will tend to opt for a short-term benefit in preference to a long-term one of greater value. Kagel et al. (1986) explain this by proposing that animals discount the value of future rewards, and that the rate of discount decreases with time. An advantage of the expected hunger model-II is that this phenomenon is accounted for without recourse to additional assumptions concerning the degree or variability of a discount function. Kagel et al. also propose that hungry animals discount future rewards more steeply than do better fed animals. Again, this proposal follows naturally from the expected hunger model.

As Kagel et al. point out, the tendency to opt for the short-term advantage is not necessarily a sub-optimal foraging tactic. On the contrary, it may be evolutionarily advantageous. For example, in the natural world, promises of food at some time in the future are not always fulfilled. The farther off the prospect, the more uncertain it becomes, and the greater the chances of other factors interposing themselves between

the animal and its goal: dying of starvation might be one such factor. Lea (1979) proposes another reason why animals might prefer immediate to deferred gratification: "Darwinian fitness is not served by waiting an indefinitely long time for an indefinitely large prey, for faced with that prospect it would be better to leave foraging altogether, and perhaps go and procreate." This is an important point which is often ignored in operant conditioning experiments. When, for example, an experimenter imposes a delay after a reward (before the next foraging cycle begins), s/he intends it as an unadulterated cost, time wasted. In the natural world, animals may usually choose how they spend their time. They are not, as in the Skinner box, obliged to do nothing. Having chosen the immediate reward, an animal may lose the benefit of a larger reward later, but in compensation it wins time. Only in the peculiar circumstances of an operant conditioning experiment is this time something to be endured rather than used.

In section (5b) the expected hunger model-II was applied to a result of Abarca and Fantino (1982). It is known (Lea, 1979) that there is a seemingly non-optimal bias among pigeons to reject a certain offer of a reward with a long handling time and prefer to search for a reward with a shorter handling time, but one which the animal has only a 50% chance of finding. Abarca and Fantino found that when handling times were changed from fixed interval to variable interval schedules, this bias was eliminated and birds made optimal foraging decisions. This result would follow if the value of a reward was a negatively accelerated decreasing function of time. Evidence for such a relationship has come from a number of sources (e.g. Pubols, 1962), and it is inherent in the expected hunger model (see Fig. 3b, curve 4). In a further experiment in which both handling times and search times followed variable interval schedules, the authors again found near optimal performances. In this case, the expected hunger model, or any model in which reward value and time are related by a convex function, predicts that pigeons should again show some bias towards the more variable option.

The main features of the expected hunger model are, that the value of a food item increases with its size and decreases with its delay (curves 1 and 4 of Fig. 3b); that these relationships are asymptoting curves (though not simple exponentials); and that the steepness of the slope depends upon the animal's food needs. The model has been presented graphically because that was how it was conceived (and I find graphs easier to follow than

equations). In consequence the mathematics are all based on trigonometry, but they need not be.

Appendix 1: an alternative expression of the absolute difference in expected hunger between constant and variable stations.

In the case where both food size and delay are varied proportionately (Fig. 2c), expected hunger in the constant patch is given by,

$$\frac{(T^2+Y^2)^{1/2}.\sin\alpha.(z+b) \quad - \quad \sin\alpha.\cos\alpha.(z+b)^2}{2}$$

Expected hunger in the variable patch is given by

$$\frac{(T^2+Y^2)^{1/2}.\sin\alpha.(z) \quad - \quad \sin\alpha.\cos\alpha.(z)^2}{4}$$

$$+ \frac{(T^2+Y^2)^{1/2}.\sin\alpha.(z+2.b) \quad - \quad \sin\alpha.\cos\alpha.(z+2.b)^2}{4}$$

The difference is therefore,

$$\frac{\sin\alpha.\cos\alpha.b^2}{2}$$

and since $b^2 = p^2 + q^2$, where p^2 is the variance of food size and q^2 is the variance of delay in the variable patch, then the difference is

$$\frac{\sin\alpha.\cos\alpha.(p^2 + q^2)}{2}$$

Appendix 2: an alternative method of using expected hunger to achieve optimal foraging

The expected hunger model, was adapted (in section 2) to achieve near optimal feeding rates in an environment of depleting patches. In the modified (EH-II) version "hunger" is no longer measured in relation to the energy budget line (which is constant) but in relation to the current average feeding rate, which changes as the animal visits more patches. Thus "hunger" becomes a relative, rather than absolute quantity; as long as a bird is feeding at the best rate possible within a given environment, then its "hunger" is zero, even though the bird may not yet have achieved it's necessary feeding rate. This conception of "hunger" is intuitively unsatisfying. We could overcome intuitive objections by calling this dimension by another name and leaving the mathematics intact. Alternatively, we can keep our conception of "hunger", and change the way the model works. This has been done in the model (EH-IIa) described in Figure 15, but it is a more complex model.

"Hunger" is properly measured as the distance (FH) from the budget line and expected hunger is given by the area of triangle FGH. As in the previous model (EHa) the goal point G is a point along the budget line given by extrapolating the current feeding rate for the environment. Additionally, the animal takes into account how long (FJ) it should take to reach its goal at the current feeding rate, and how much food it can expect to obtain (JG). The animal leaves a patch when the ratio (R) given by $\Delta FGH/\Delta FGJ$ is at a maximum. Where ΔFGH (expected hunger) is given by eq. (2.2),

$$\frac{(T.(y+y_{\times}) - Y.(t+t_{\times})).(Y^2 - Y.(y+y_{\times}) + T^2 - T.(t+t_{\times}))}{2.(T^2 + Y^2)}$$

and ΔFGJ is given by

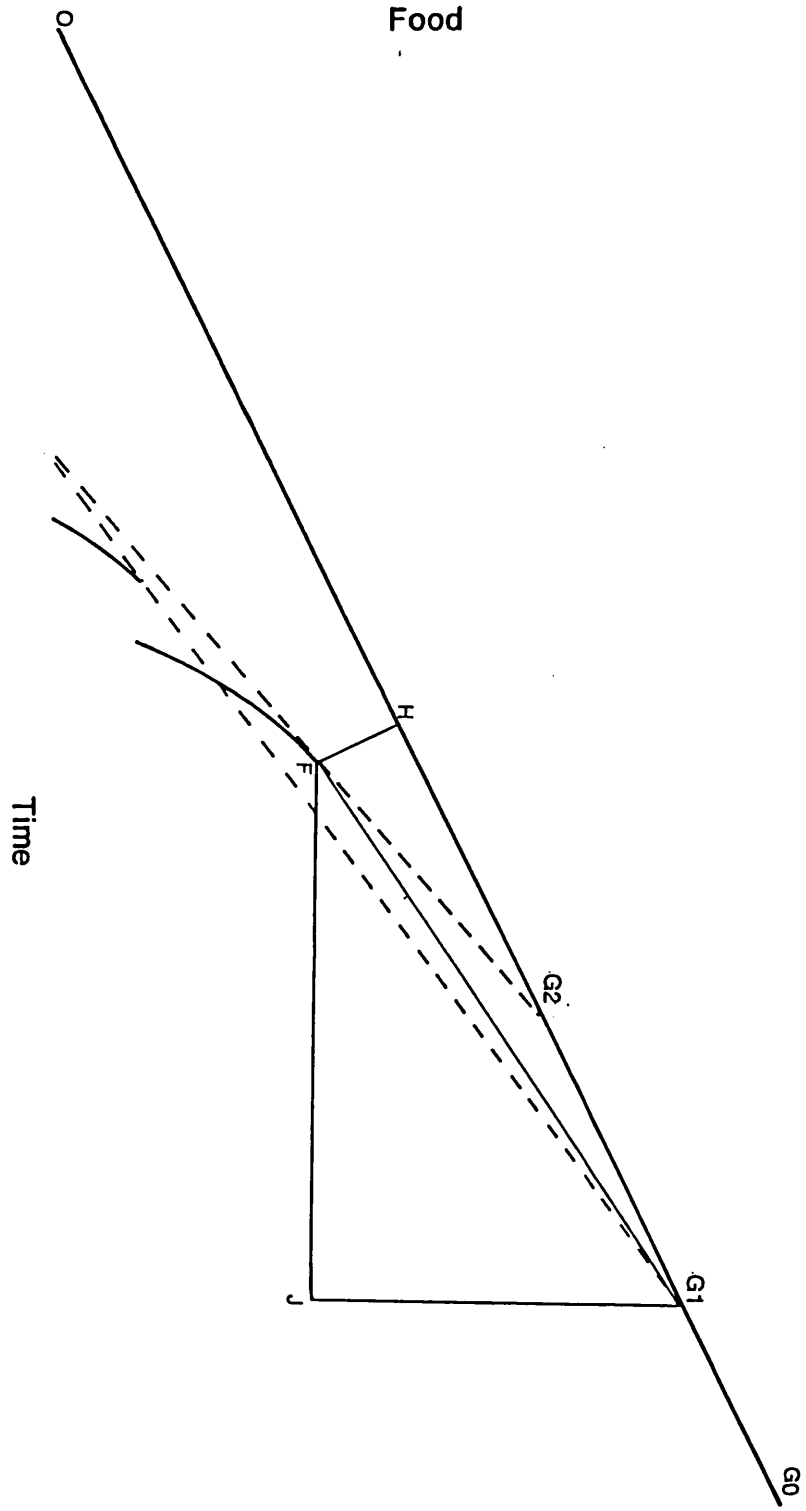
$$\frac{(T - (t+t_{\times})).(Y - (y+y_{\times}))}{2} \qquad (A2.1)$$

T = total time and Y = total food from the origin (O) to the goal point (G); $y = F.(1-e^{-\nu.t})$, the amount of food eaten in the current patch in time t; $y_{\times}$ = sum of food eaten in previous patches; t = time spent in current patch; and $t_{\times}$ = sum of time spent in the environment up to entering the current patch. Thus the ratio R is given by

$$R = \frac{\Delta FGH}{\Delta FGJ} = \frac{Y.(T.(y+y_{\times}) - Y.(t+t_{\times}))}{(T - (t+t_{\times})).(T^2 + Y^2)} + \frac{T.(T.(y+y_{\times}) - Y.(t+t_{\times}))}{(Y - (y+y_{\times})).(T^2 + Y^2)} \qquad (A2.2)$$

Fig. 15

Another version (IIa) of the expected hunger model applied to the problem of how long to stay in a depleting patch, surrounded by other identical unexploited patches at identical distances. After a period of deprivation, the animal enters the environment at point A and travels T_t seconds to the first patch. It samples this patch for 10 sec, and on the basis of its average feeding rate thus far, sets itself a goal point G_1, where its energy budget would be in balance. The animal travels to the next patch and leaves it when its expected hunger (in relation to G_1) increases, or its expected satisfaction decreases. On leaving the patch, it re-evaluates its average feeding rate, and extrapolates it to arrive at a new goal point G_2.


Food
O
Time
H
F
G2
G1
J
G0

Since R is maximal when dR/dt = 0, then the optimal time (t) to spend in a patch satisfies the equation,

$$0 = \frac{dR}{dt} = \frac{Y.(F.T.v.e^{-v.t} - Y)}{(T - (t+t_x)).(T^2 + Y^2)} + \frac{Y.(T.(y+y_x) - Y.(t+t_x))}{(T - (t+t_x))^2.(T^2 + Y^2)}$$

$$+ \frac{T.(F.T.v.e^{-v.t} - Y)}{(Y - (y+y_x)).(T^2 + Y^2)} + \frac{(F.v.e^{-v.t}.T).(T.(y+yx) - Y.(t+t_x))}{(Y - (y+y_x))^2.(T^2 + Y^2)} \quad (A2,3)$$

which may be solved for t by iteration.

Table 6. The models' performances in three environments of mixed depleting patches, and one environment with variable travelling times, compared with optimal performance, given by MVT and that using a constant residence time rule.

	Rate of feeding (food units/sec)			
	Expected Hunger Model-IIa	Expected Hunger Model-II	Optimum (MVT)	Best fixed residence time (t)
Environment 1 (variable v)	,0284945	,0286059	,0286187	,0285635 (64,3847 sec)
Environment 2 (variable F)	,0304390	,0304509	,0304765	,0286223 (64,627 sec)
Environment 3a (variable v and F)	,0320384	,0320683	,0320962	,0291729 (63,461 sec)
3b	,0350885	,0351168	,0351516	,0299551 (60,167 sec)
Environment 4 (variable t_t)	,0285989	,0285987	,0286223	,0286223 (64,627 sec)

Each of the first three environments consisted of 999 patches (333 of each patch type) encountered in random order, and separated by 20 sec travelling time. In Environment 1, F was always 6, and v was ,007, ,008 or ,009. In environment 2, v was always ,008 and F was 4, 6 or 8. In Environment 3a F = 4 and v = ,007; F = 6 and v = ,008; or F = 8 and v = ,009; in environment 3b F = 4 and v = ,005; F = 6 and v = ,008; or F = 8 and v = ,011. In the fourth environment F was 6, v was ,008, and the travelling times were either 10, 20 or 30 sec. Parameters of the models were as for Table 1. For calculation of optimal feeding rates see text.

Table 7. The models' performances in three "stochastic" environments of mixed depleting patches, compared with the theoretically optimal performance, given by MVT and that using a constant residence time rule.

	Rate of feeding (food units/sec)			
	Expected Hunger Model-IIa	Expected Hunger Model-II	Optimum (MVT)	Best fixed residence time (t)
Environment 1 (variable v)	,0269789	,0275675	,0286187	,0285635 (64,3847 sec)
(unweighted)	(,0265885)	(,0266100)		
Environment 2 (variable F)	,0285515	,0289596	,0304765	,0286223 (64,627 sec)
(unweighted)	(,0277217)	(,0277447)		
Environment 3a (variable v and F)	,0298032	,0299842	,0320962	,0291729 (63,461 sec)
(unweighted)	(,0290178)	(,0289152)		
3b	,0323346	,0319062	,0351516	,0299551 (60,167 sec)
(unweighted)	(,0314739)	(,0315509)		

Food was obtained in discrete units of variable size and at variable intervals in a pseudo-stochastic manner described in the text. Each of the first three environments consisted of 999 patches (333 of each patch type) encountered in random order, and separated by 20 sec travelling time. In Environment 1, F was always 6, and v was ,007, ,008 or ,009. In environment 2, v was always ,008 and F was 4, 6 or 8. In Environment 3a F = 4 and v = ,007; F = 6 and v = ,008; or F = 8 and v = ,009; in environment 3b F = 4 and v = ,005; F = 6 and v = ,008; or F = 8 and v = ,011. Parameters of the model were as for Table 2. The weighting factor W (see text) was 0,5. Results obtained without using a weighting factor are shown in brackets.

Appendix 3: an alternative measure of expected hunger.

Section 4 assumes that an animal evaluates a trial on the basis of its expected hunger immediately upon obtaining a food item. It may be more realistic to assume that the expected hunger associated with a particular trial is averaged throughout the trial. Instead of measuring H at a particular point within a trial or at the end of a trial, it may be integrated over the time course of the whole trial and the average taken. Thus if H at a particular time is given by equation (2.2) of section 2,

$$H = \frac{(y.T - t.Y).(Y^2 - y.Y + T^2 - t.T)}{2.(T^2 + Y^2)}$$

Then the average (H_{av}) is,

$$H_{av} = (t_n - t_o)^{-1} . \int_{t=to}^{t=tn} H.dt$$

$$= \frac{1}{(t_n - t_o)} . \left[\frac{t.(y.T.Y^2 - y^2.T.Y + y.T^3)}{2.(T^2 + Y^2)} \right]_{t=to}^{t=tn}$$

$$- \frac{t^2.(y.T^2 + Y^3 - y.Y^2 + T^2.Y)}{4.(T^2 + Y^2)} + \frac{t^3.Y.T}{6.(T^2+Y^2)} \Bigg]$$

(A3.1)

where t_o is the time at which a food unit is obtained and t_n is the time at which the trial ends. In experiments such as Caraco's, food is found at the start of a trial and therefore $t_o = 0$. When food size and delay between trials are manipulated together, then the adavantage of choosing the constant station (e.g. 2 seeds followed by a 2 min delay) over the variable station (e.g. 1 seed or 3 seeds followed by 1 or 3 min delay) is given by,

$$H_{av}(\text{constant}) - H_{av}(\text{variable}) = H_{av}(y_2, t_2) - \frac{[Hav(y_1, t_1) + H_{av}(y_3, t_3)]}{2}$$

(A3.2)

where y_1 and y_3 are, respectively, the small and large rewards obtained at the variable station, and y_2 is the reward obtained at the constant station. Similarly, t_1 and t_3 are durations of trials at the variable station and t_2 is the duration of trials at the constant station. Since

$$y_2 = \frac{y_1 + y_3}{2} \quad \text{and} \quad t_2 = \frac{t_1 + t_3}{2},$$

then the difference in H_{av} may be expressed as

$$\left[\ 3.T.Y.(y_3-y_1)^2 - \frac{3}{2}.(Y^2-T^2).(t_3-t_1).(y_3-y_1) - T.Y.(t_3-t_1)^2\ \right].\ \frac{1}{24.(T^2+Y^2)} \qquad \text{(A3.3)}$$

For the case where T=Y, this simplifies to,

$$H_{av}(\text{constant}) - H_{av}(\text{variable}) = \frac{3.(y_3-y_1)^2 - (t_3-t_1)^2}{48}$$

For the case in Figure 7a (points x,y, and z) where the feeding rate at the end of a trial is the same regardless of the station chosen and this feeding rate is sufficient to achieve the daily energy budget i.e.,

$$\frac{y_3}{t_3} = \frac{y_1}{t_1} = \frac{Y}{T} \quad (= 1)$$

then the difference in EH_{av} will be positive. Therefore, birds should prefer the constant station, in agreement with Caraco's findings. When the feeding rate at the end of a trial is inadequate to meet the energy budget (Fig. 7b) then the variable station should be preferred for

$$\frac{y_n}{t_n} < \frac{1}{3^{1/2}}$$

Chapter 5

A role for cognition

1. INTRODUCTION

1.a. From rules-of-thumb to reasoning

Animals are not omniscient. They do not have perfect information about where food may be found, how long it will take to find it, how much there is, or when it will run out. Nevertheless, in the process of finding food they acquire imperfect information about all of these things. If it pays animals to be competitive, it should pay them to use this information.

A bullfinch, for example, obliged to choose between two sunflower fruits can only know exactly how long it will take to crack the husk, or the size of the kernel inside, after it has cracked the husk and eaten the kernel. The size, weight and shape of the sunflower fruits, however, are proximal cues to their profitability -- big, fat fruits have big kernels but are harder to crack -- and by using them, the bird can (and often does, Greig-Smith and Crocker, 1986) make an informed choice about which fruit is likely to be the more profitable. The bird may therefore employ a rule of thumb (ROT) which, although not as successful as having perfect foresight, will minimise foraging costs given the information available to it. ROTs used in this sense do not imply that the animals employing them are behaving sub-optimally, but rather that they are foraging as best they can given their imperfect knowledge (Krebs, Stephens and Sutherland, 1983).

There is another sense in which the ROT concept is used in the literature which implies a compromise in feeding success whereby proximate cues about food distribution are not being used to the animal's best advantage. ROTs used this way (e.g. Green, 1980, 1984; Howell and Hartl, 1980; Janetos and Cole, 1981; Ydenberg 1984) are assumed to be adequate approximations to the optimal strategy but have the advantage of being simple. They require less processing of information by the animal which is time consuming and may be costly. For example, animals are unlikely to have perfect memories and their estimation of patch quality may therefore be mistakenly biased towards recent events. A transient run of bad luck may be mistaken as a sign that the patch is depleted. Nevertheless,

estimates weighted in favour of recent experience are likely to be fair approximations to the optimal strategy (Harley, 1981).

In the first sense, ROTs are seen as the result of environmental constraints or the individual's limited experience within the environment. ROTs in the second sense are seen as arising from constraints within the individual. In both senses, ROTs, being concerned with proximate mechanisms, differ from classical optimal foraging theory in that they describe a foraging strategy from the animal's point of view, rather than in terms of the ultimate implications for rate of food intake or evolutionary fitness. Environmentally constrained ROTs should still be optimal within an animal's given circumstances, whereas individually constrained ROTs are addressed to those rules, optimal or not, that the animal actually uses while foraging.

Thus, where an experimental animal is seen to be foraging more or less optimally, we often do not know what information it is using or how it uses it in deciding how to forage. The experimenter knows what the animal should do because s/he has set the parameters and has a computer to solve the relevant equations. The implausibility that animals solve the same equations has led some authors to propose that ROTs should be simple and robust (efficient over a wide range of conditions). But this does not necessarily follow.

Glasser (1984), discussing the choice of food types, reiterates the argument that where food is reliably abundant it pays to specialise on the best kinds; where food is scarce, to generalise; and where abundance is variable, to be flexible, specialising and generalising in proportion to abundance. He points out that for a truly obligate specialist, such as a parasite, or an obligate generalist, such as a suspension feeder, information on the relative abundance of food types is redundant. However, many animals can improve their feeding success by using information about the distribution of particular food types. Given that an animal has a fixed investment in brain hardware and a limited time it is prepared to spend processing information, then its best feeding strategy will depend on the particular distribution of food it can expect to face in its normal foraging environment.

A specialist feeding in a constant environment should use a specialised feeding strategy. It need not be especially simple or robust. For a generalist feeding in an unpredictable environment, the best feeding strategy would seem to be one that is robust (but not necessarily simple),

performing adequately in most situations. Since, in both these instances, the animal needs only a single feeding strategy, the strategy should be as sophisticated as its budget for information processing allows.

Stephens et al. (1986) make the point that "simplicity" is a slippery concept. "In their collective haste to find simple and cheap rules (e.g. Janetos and Cole, 1981), many authors have ignored the possibility that the rules required to approximate long-term rate maximisation need not be complicated or expensive. For example, a decision rule based on continually updated acheived rates associated with various activities may be all that is required. A running tally might be simple and cheap to operate and maintain. The chief problem is that the intuition of biologists about which rules are simple and cheap has been unreliable. Animals can often perform more-subtle tasks than an intuitive view of their simplicity allows..."

A complex feeding strategy need not imply a "cognitive" one. On the contrary, the more likely that a single ROT (complex or simple) will do, the more likely that it will be "hardwired" or "mindless". Charnov (1976) for example, has shown that the readiness of a mantid to attack passing flies depends on the fullness of its gut, which is an estimate of prey abundance. Ollason (1980) presents an algorithm which enables an animal to stay the optimum patch time in an environment of depleting patches. As was outlined in chapter 4 , the animal's memory takes the form of a leaky bucket in which the contents are disappearing at a rate proportional to their level in the bucket. (The more an animal has in its memory, the quicker it forgets.) An animal remembers what it has eaten, and so, within a patch, memory contents increase until they are counterbalanced by the rate of forgetting. Since the patch is depleting, the level begins to fall; at which point the animal leaves the patch. Thus, according to Ollason "all an animal needs to do is remember and to leave the patch if it is not feeding as fast as it remembers doing." Similarly Waage (1979) suggests that the parisitoid wasp *Nemeritis* leaves a patch when its sensitivity to its host odour declines below some threshold and that sensitivity itself varies according to the wasp's success in the patch.

These models are generally referred to as simple ROTs (e.g. Shettleworth, 1984). But it is not inherently a simple matter to monitor a rate of memory change or to differently react to a smell according to how long it has been smelt and according to the outcome of some other behaviour which is being performed the while. The crucial point about these models is not that they are simple (they are not) but that they are

non-cognitive - fixed mechanisms that operate behind the scenes of what might be an essentially mindless animal.

Simple ROTs, I would argue, are more suited to animals which make cognitive decisions about feeding strategy. "Cognitive", here implies an animal which is flexible in its choice of feeding strategy, or is able to modify a given feeding strategy to suit local conditions (See Kamil 1984,). Kamil and Yoerg (quoted in Kamil 1984), Lima (1985), and Cowie (1979) have shown that birds are capable of adopting different feeding strategies under different conditions of food distribution. Kacelnik (quoted in Houston, Kacelnik and McNamara, 1982) suggests that great tits adjust the amount of time spent sampling (before exploiting) two patches of unknown quality, according to the amount of time (their "time horizon") they expect to have available for foraging before the experimenter interrupts them. Greig-Smith (1984) has shown that bullfinches will select and handle sunflower fruits differently in a cage with a solid floor than one where dropped seeds fall out of reach through a barred floor. For animals which forage in environments which are too variable for a specialised feeding strategy to perform well, but stable enough to pay the animal to take account of local conditions, then cognitive rules for adapting its feeding strategy would seem to be implicated; and, given limits on information processing, simple rules would be preferable. These rules would describe how an animal chooses one feeding strategy rather than another or how it modifies a particular strategy. For example, an animal might adjust the weighting given to recent events (the size of the hole in Ollason's leaky bucket, the memory factor in Harley's Relative Pay-off Sum rule). Or in Green's example of a bayesian bird systematically searching non-depleting patches, and leaving them after t bits of the patch have been searched given n food items have been found -- a cognitive rule would tell it how to vary t given n, and thus arrive at the best relationship between them for a particular distribution of food between patches.

1.b. Reasoning ability

Several authors have recently emphasised the role of cognition in foraging behaviour (Kamil 1984, Kamil and Yoerg 1982, Menzel 1981, Shettleworth 1984). There has been a general revival of interest in animal cognition (see for example the papers in Roitblat et al, 1984), and not merely in the primates and higher mammals; the possibility of cognition in birds is being treated seriously (see Crocker, 1985).

There are an increasing number of reports on the abilities of birds to master complex learning problems (e.g. learning set formation in the Greater Hill Myna (Kamil and Hunter, 1970) and in Blue Jays (Hunter and Kamil, 1971), oddity concept fromation in Pigeons (Lombardi et al., 1984), spontaneous tool-use in Rooks (Reid, 1982), class concept formation in the African Grey Parrot (Pepperberg, 1983), insight in Pigeons (Epstein et al., 1984)). For more than 25 years, the laboratory of L.V. Krushinskii at Moscow State University, has been investigating the "elementary reasoning ability" of mammals, birds and reptiles (for reviews, see Krushinskii, 1977; and Krushinskii et al., 1982; and, in English, Krushinskii et al., 1968; Krushinskii, 1973; Zorina, 1982).

According to Krushinkii, reasoning ability differs from the learning ability shown in classical and operant conditioning. In operant conditioning experiments, an animal is repeatedly presented with a stimulus and rewarded for an appropriate response; learning takes the form of a gradual association between the two. Elementary reasoning ability, on the other hand, is defined as "the ability of an animal to grasp simple causal relationships between objects and phenomena in its environment and to apply this knowledge in new situations," (Krushinskii et al., 1982). Whereas the formation of conditioned reflexes or habits becomes evident only after many trials, the presence or absence of reasoning ability should be demonstrable within a single trial. "Reasoning ability" would thus seem to share much in common with "insight" (Kohler, 1925).

In a number of studies (see the references above), Krushinskii and his co-workers have claimed that animals are able to solve certain kinds of logical problems at the first attempt. In these studies, the possibility of learning was eliminated by allowing each animal only one attempt at a particular problem. This means that many animals must be used. Another drawback is that when individuals fail to solve a problem, it is not clear

whether they lack "reasoning ability," or whether, for example, they are upset by the novelty of the apparatus or the stimuli. The present experiment was designed not to encourage reasoning at the expense of habit-formation, but to separate their effects.

2. RATIONALE

The birds (6 Hooded Crows) were given two types of problem to solve -- a "causal" and an "arbitrary" problem. In both kinds of problem, the birds were presented with two containers of different colours, one of which concealed food. In the arbitrary problem, the containers also differed in shape; one was apple-shaped and the other was shaped like an hour-glass (see Fig. 1). In the causal problem, the containers were the same shape but one was opaque while the other one was transparent. Thus in both problems the birds could use either or both of two cues to distinguish between the containers -- transparency and colour in the causal problem, shape and colour in the arbitrary problem.

The "causal" problem is so-called because its solution is deducible from the available cues. When a bird is presented with a transparent and an opaque container and no food is visible in the transparent container, then a reasoning animal should choose to investigate the opaque container. There is no causal reason why the colours of the containers should matter.

The "arbitrary" problem is so-called because there is no causal reason why either colour or shape should be especially likely to signal the presence of food.

Training occurred in two main stages. In the causal problem, the food reward was always hidden under the opaque container and the problem was repeated until the bird had solved it according to a pre-established criterion. In a second stage, the food was again hidden under the opaque container, but the colours were reversed. For example, a bird presented with a blue transparent container and a yellow opaque container in stage I, was then asked to choose between a yellow transparent and a blue opaque container in stage II. If, in stage I, the bird attends mainly to the causal cue (transparency/opacity), then reversing the colours should not impede its performance and it should rapidly learn the new variation. If, however, the bird simply learns to respond to the most salient feature of the rewarded container, then the container's colour may be as important a

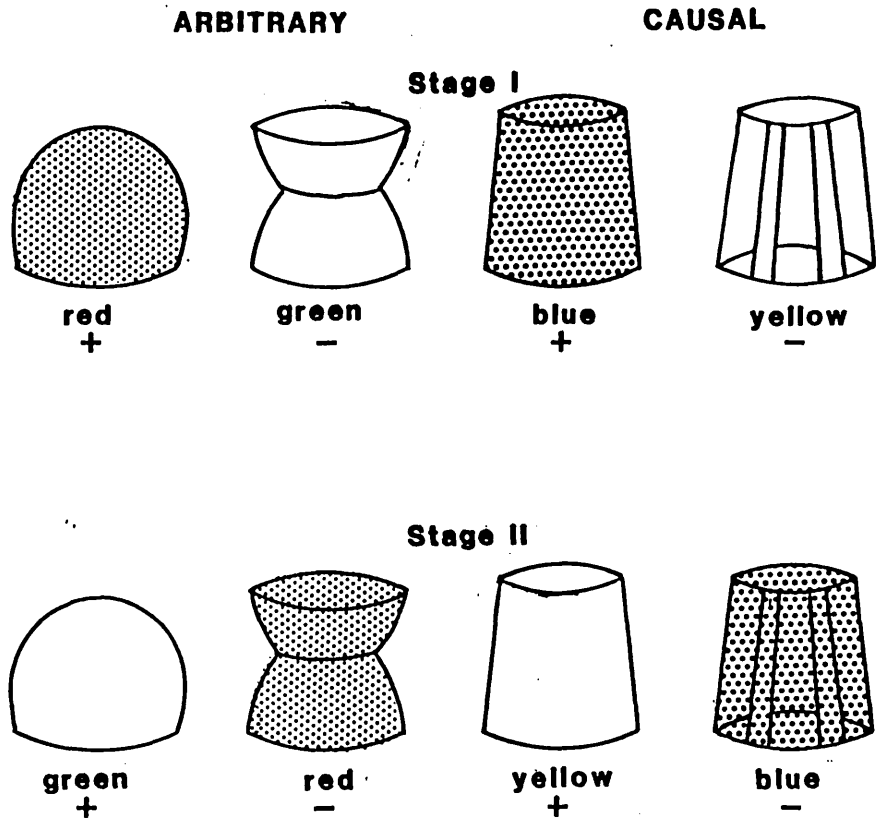


Fig. 1.

The experimental stimuli.
+ indicates that the object concealed food
- indicates the absence of food.

cue as its transparency. When the colours of the rewarded and unrewarded containers are swapped over, birds may be misled.

The procedure for the arbitrary problem was similar except that the experimenter arbitrarily chose which container would contain food. Thus, if food was always hidden in the apple-shaped container, and the bird was presented with a green apple and a red hour-glass in stage I, then in stage II it was given a red apple and a green hour-glass.

The prediction therefore, is that birds which take more notice of causal cues than arbitrary cues should perform better in stage II of the causal problem than in stage II of arbitrary problem.

3. METHOD

3.a. Subjects

Six Hooded Crows (*Corvus corone cornix*) were used, all younger than 11 months old when the experiments began. The birds, provided by Moscow Zoo, had been caught as nestlings and had already taken part in another experiment using the same apparatus.

3.b. Apparatus

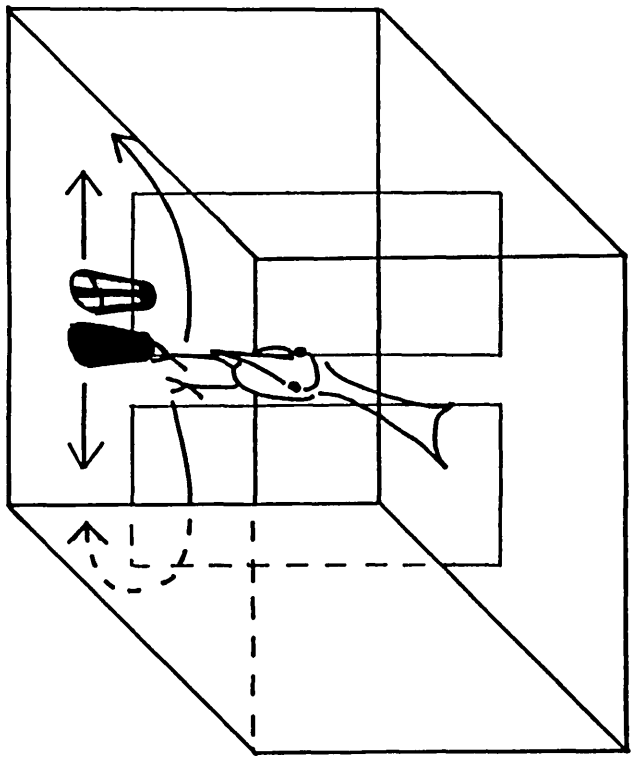
The experimental apparatus (Fig. 2) was a chamber (1.2 x 1.2 x 0.6 m) with a mesh roof and was open at one end where the experimenter sat. The chamber was divided by a clear perspex screen, behind which the bird was placed. In the middle of the screen was a slit, wide enough for the bird to poke its head through. At either end of the screen was room enough for the bird to pass through to the front half of the chamber where food was hidden under one of two containers. The containers were made from transparent tinted plastic picnic glasses or from coloured plastic balls (Fig. 1).

3.c. Procedure

Mealworms were placed in a small foodcup and shown to the bird through the slit, thus ensuring that the bird was attentive and standing

Fig. 2.

The experimental apparatus.



in the centre of the chamber. When the bird tried to peck at the worm, the foodcup was withdrawn out of reach behind an opaque screen and hidden under one of the two experimental containers. The containers themselves rested upon two centrally placed platforms which, after the opaque screen was removed, were moved apart and rotated by a pulley mechanism underneath to either side of the chamber. The bird was then free to move around either side of the perspex screen to investigate one or other of the containers. It was not allowed to investigate both containers. The foodcup was concealed in the left-hand or right-hand container according to a pseudo-random sequence in which food never appeared in the same place more than three times in succession, and at the end of every ten trials had appeared five times on the left and five times on the right. Trials were performed one immediately after another, each trial taking about one minute. Before each experimental session, the birds had been deprived of food for 24 hours.

Three birds (Green, Blue, and Silver) were given the causal problem first and three birds (Neutral, Grey and Red) given the arbitrary problem first. The arbitrary problem consisted of two stages and the causal problem of three, all performed during the same experimental session. The causal and arbitrary problems and the later control experiments birds were carried out within about week of each other. Birds were considered to have mastered a given stage when they performed better than would be expected by chance at the 0.01 level. This could be met either by 10 successive correct choices (or 11 or 12 in succession if the total number of trials exceeded 20 or 32, respectively), or by the total number of correct choices exceeding incorrect choices by the appropriate margin. (The actual significance level is unimportant. It is important only that a consistent learning criterion be applied throughout.) The point of employing two criteria simulataneously was to minimise extreme cases of birds requiring many trials to satisfy one criterion, when they had already fulfilled another equally valid criterion of proficiency.

Stage I

The birds were repeatedly presented with the same problem at one-minute intervals until they had solved it or until the number of trials reached 50. There was a five minute interval between stages I and II.

Stage II

The colours of the stimuli in stage I were swapped over and the number of trials needed to relearn the problem was noted. In the causal

problem, birds underwent a further stage (III), after a five minute interval.

Stage III: a "trick question."

In the causal problem, the foodcup was always hidden under the opaque container, the colour of which changed from stage I to stage II. A perfectly rational animal having successfully completed these stages may be thought of as following a rule of the kind "If there is no food visible in the the transparent container, then investigate the opaque container." Howevér, since food is never presented in the transparent container, the bird may, by the end of the experiment, be following a simpler rule of conditioned association such as "always choose the opaque container."

To test this possibility, the birds, having completed stage II of the causal problem, were required, to undergo a "trick question." Here, the containers and procedures were exactly as for stage II except that the foodcup was always hidden in the transparent container and was always visible. A rational animal should choose to investigate the transparent container where it may actually see that food is present, rather than risk searching the opaque container which may or may not conceal food. An animal which has "blindly" learned to associate the opaque container with food is likely to continue in the habit, at least for the first few trials.

Control Experiment 1: colour as the correct cue.

In the arbitrary problem above, shape is the significant feature of the container concealing food; its colour is irrelevant. Because of a possible bias in the crow's sensory system or because of earlier experience, birds may be more sensitive to colour than to shape. Thus they may find it especially difficult to ignore colour and attend to shape when there is a conflict of cues in stage II. Therefore the arbitrary problem was repeated but this time the colour of the correct container was held constant over both stages while the shapes were swapped.

Control Experiment 2: pattern as the correct cue.

Examination of Figure 1 shows that the difference between the containers in the causal problem is not limited solely to their transparency/opacity and colour. The transparent containers also have four opaque stripes to accentuate their colour. It is possible that the birds may learn to pay attention to the more abstract cue of "pattern", choosing the *plain* (opaque) container rather than the *striped* (transparent) container. To check for this possibility, the containers used in the causal experiment were all made opaque. Birds were randomly assigned colours and

patterns in stage I. In stage II, the pattern of the correct container (plain or striped) was held constant while the colours were reversed.

4. RESULTS

During stage I (Table 1), the birds did not learn to solve the causal problem significantly more quickly than they learned to solve the arbitrary problem ($t = 0.7$, $df = 5$, ns). However, when the colours of the containers were reversed in stage II (Table 2) proficiency at the causal problem was regained significantly more quickly than the arbitrary problem ($t = 2.18$, $df = 5$, $p < .05$, 1-tail test). Similarly, when the arbitrary problem was repeated in the control experiments treating colour and pattern as the correct cues, performance was significantly worse than that for the causal problem.

Examining the data for individual performances (Tables 2 and 3), it is interesting to note that birds which performed poorly in stage II of the arbitrary problem (birds "neutral" and "green") when shape was the correct cue, performed very well in the control experiment when the correct cue was colour. Bird "blue", on the other hand, performed much better when the correct cue was shape rather than colour. All birds did rather badly when they were required to identify the correct container according to its pattern.

Table 3 shows that although all birds solved the "trick question" relatively quickly, only two birds ("red" and "grey") transferred allegiance immediately and completely from the opaque container (where food *may* have been hidden) to the transparent container where food was visible. This result suggests that having solved the causal problem, birds proceeded to act out of habit rather than reason.

Table 1.

STAGE I

NO. OF TRIAL ON WHICH FINAL MISTAKE WAS MADE

PROBLEM CORRECT CUE	Causal Opacity	Arbitrary Shape	Difference
BIRD			
Grey	2	18	+16
Neutral	8	4	- 4
Silver	9	11	+ 2
Red	2	13	+11
Green	15	4	- 9
Blue	13	13	0
			t = 0.7 ns

Comparison, as gauged by the number of the trial on which the final mistake was made before achieving the learning criterion, of birds' abilities to learn stage I of the causal and arbitrary problems. The lower the number, the better the performance. Data for stage I of the two "arbitrary" controls are not included because birds had already met the colours and/or shapes in the original causal and arbitrary problems and required extra trials to overcome learned preferences.

Table 2.

STAGE II

NO. OF TRIAL ON WHICH FINAL MISTAKE WAS MADE

PROBLEM CORRECT CUE	Causal Opacity	Arbitrary Shape	Arbitrary Colour	Arbitrary Pattern
BIRD				
Grey	2	8	17	25
Neutral	0	12	0	22
Silver	6	12	15	33
Red	7	50	18	20
Green	0	12	0	21
Blue	0	0	27	23
		t = 2.14 ($p < 0.05$)	t = 2.49 ($p < 0.05$)	t = 11.06 ($p < 0.001$)

As for Table 1, but the comparison here is for Stage II, and includes the two "arbitrary" controls, where colour and pattern were deemed to be the correct cues.

Table 3.

BIRD	EXPERIMENT	TRIAL NO. (10 / 20 / 30 / 40 / 50)
Grey	Causal	+-++++++++++
	Arb. (shape)	++++++--+++++++
	Trick Q.	++++++++++
	Arb. (colour)	++-++++-+-++++++-+++
	Arb. (pattern)	----------++--+-+-+++-+-++-++++++++++++
Neutral	Causal	++++++++++
	Arb. (shape)	---++-++----++++++++++
	Trick Q.	+-+--++-++++++++++
	Arb. (colour)	++++++++++
	Arb. (pattern)	-+-++-+--+--+-++++-+--++++++++++++
Silver	Causal	++-++-++++++++++
	Arb. (shape)	-+-+++--+++-++++++++++
	Trick Q.	+-+++++++-++++++
	Arb. (colour)	+++++-+-++++++-+++
	Arb. (pattern)	+----+-+-++--+-++-+++++-++-++--+-++++++++++++
Red	Causal	+-+--+-++++++++++
	Arb. (shape)	----+---+-+--------++-+--+-++-+---+-++-+---+-+++-+
	Trick Q.	++++++++++
	Arb. (colour)	+-----+--+---+-+--++++++++++++
	Arb. (pattern)	+---+-+--++-++-+-++-++++++++++++
Green	Causal	++++++++++
	Arb. (shape)	+-----+--+--++++++++++
	Trick Q.	+++-+-+-+++-+++-++++++++
	Arb. (colour)	++++++++++
	Arb. (pattern)	-+--++--++++-+++-++--++++++++++++
Blue	Causal	++++++++++
	Arb. (shape)	++++++++++
	Trick Q.	---++++++++++
	Arb. (colour)	----------+-+-+++-+--++--+-++++++++++++
	Arb. (pattern)	--------+--+-+-+--++++-++++++++++++

Raw data for stage II of all the problems and for stage III of the causal problem -- the "trick question." + = correct choice, - = incorrect choice. Words in brackets denote which cue was deemed by the experimenter to be the correct cue.

5. DISCUSSION

The results suggest that for young crows, problems with a causal solution are not inherently easier to solve than problems with arbitrary solutions. However, having identified the correct container, the birds in this experiment appeared more likely to associate the presence of food with its causal features (the opacity of the correct container compared with the transparently empty container) than with its arbitrary features (its colour). Thus when the two cues, both signifying the presence of food in stage I, were arranged to conflict in stage II, the birds were more likely to attend to the causal cue. That several birds, having grown accustomed to choosing the opaque container in stage II of the causal problem, failed to make an immediate switch to the transparent container when food was placed there in stage III (the "trick question"), suggests that habit also played a role in the birds' behaviour.

One explanation of these results is that the transparency/opacity dimension was simply more salient than the colour, shape or pattern of the stimuli. It is hard to think of a reason why this should be so. Animal sensory systems might be expected to be preferentially sensitive to those features of their environments which are biologically significant; the smell of a stimulus might be expected to have more salience for a rat than a pigeon, for example. It would be easier to think of reasons why colour, shape and pattern should have more salience for a crow than has transparency/opacity.

These findings may also be seen as supporting recent theories of animal learning which suggest that "conditioning is now best viewed not as a matter of strengthening stimulus-response associations by an automatic process called reinforcement, but rather as a matter of...learning about the relations between events, or finding out what causes or signals the occurrences of such events of consequence as food or water or danger or safety" (Mackintosh, 1984).

Williams (1982, 1984) has shown, that pigeons are sensitive to the *relative* predictiveness of stimuli signalling food rewards. Pigeons will readily learn a conditional discrimination in which, for example, food follows a red light when it occurs in conjunction with a vertical bar (but not when red occurs with a circle) and food follows a green light in

conjunction with a circle (but not with a bar). However, if the coloured light scheduled for a particular trial is illuminated during the preceding intertrial interval, birds do not learn the discrimination. The failure to learn, appears to be due to the loss of predictiveness of the coloured lights relative to the patterns, and not simply because the onset of the colour is is distant from the food reward in absolute time. When both colour and pattern were illuminated during the intertrial interval the conditional discrimination was successfully learned.

Testa (1974) argues that animals are more likely to associate events which occur closely together in space as well as time, since such events are likely to be causally related, and it would be adaptive for animals to be especially sensitive to causal relationships. In this way he explains rats' superior performance in avoiding shock in a one-way shuttlebox compared with a two-way shuttlebox. In a one-way shuttlebox the animal can expect the shock to come from a particular place and can avoid it by running in a particular direction. This is not so for a two-way shuttlebox where animals may be shocked in areas where they were previously safe and required to run to areas where they were previously shocked.

In the present experiment, both the arbitrary cue (colour) and the causal cue (transparency/opacity) were present at the same time and therefore both were equally good predictors in terms of temporal and spatial contiguity. Transparency/opacity however, provides a causal cue to presence or absence of the food reward, and birds were more likely to heed it when causal and arbitrary cues were in conflict.

Until recently, selective attention among animals to causal relations has often been assumed but not made explicit (see though Tolman, 1959). An appreciation of causality is essential to Krushinskii's definition of reasoning ability. He argues that neither instinct (which is adaptive only under very specific conditions) nor habit formation (which is adaptive only under very stable conditions) can explain the adaptiveness of animal behaviour in changing environments. We need to take account of an animal's ability to abstract, from the mass of spurious information confronting it, those elements and relations that enable it to predict, and take advantage of what is likely to happen.

Conclusion

A note on optimality

In several chapters of this thesis the behaviour of foraging bullfinches in different environments has been compared to that of a hypothetical bird attempting to maximise its rate of food intake. Very often the performances of bullfinches in these experiments fell far short of the optimal strategy.

How do we interpret this apparently sub-optimal ability to gather food? One could argue that this is evidence that bullfinches are indeed merely adequate foragers, satisficing but not maximising their food intake. Another possibility is that birds may be maximising some other or more complex function such as the rate of food intake constrained by the need to be vigilant for predators. The trouble is that there are an infinite number of candidate functions. Sooner or later one is bound to come across something that the animal does appear to be maximising. In its extreme form this is known as "the inverse optimality approach" (see McCleery, 1979). The experimenter assumes at the outset that the animal is maximising something, and by measuring behavioural costs and benefits attempts to discover what that something is. Unfortunately, there is no guarantee that the end function will be unique or that it will be biologically meaningful.

Pierce and Ollason (1987) scorn optimal foraging theory as "a complete waste of time". Their principal objection is that the theory depends on circular reasoning. On the one hand theorists seek to prove that by maximising performance in some activity animals thereby maximise their fitness. On the other hand when it happens (and it often does) that animals fail to fulfil the theorists expectations they reverse the argument. They assume that animals are maximising their fitness and modify the definition of the function-to-be-maximised. Cowie (1977), for example, found that great tits stayed longer in a series of depleting patches as the travelling time between them increased. This was in good qualitative but not so good quantitative agreement with the assumption that birds were maximising feeding rate. A much better fit was obtained when Cowie introduced the energetic costs of flying between patches. Pierce and Ollason are unimpressed by this device and I think their

dissent is understandable in this case, especially since increased travelling time did not entail increased flying. Nevertheless there is room here for legitimate debate. What some may consider an unwarranted addition brought in to fudge the predictions and save the model, others may consider a reasonable and plausible accommodation. Of course, as more assumptions are added *ad hoc*, credibility becomes strained and when it finally breaks it is time to build another model. In the meantime it is hard to blame scientists for holding on to their babies while they throw out the bathwater.

Ollason (1980) himself has been guilty of the occasional *ad hoc* assumption. He developed a model which simulated the optimal foraging strategy in Cowie's experiment, but which failed to simulate the actual behaviour of Cowie's birds, whose residence times within patches were longer than expected. He explained the discrepancy by invoking the fact the birds had been deprived of food for two hours before the experiment began. This deprivation time could be interpreted by his model as an exceedingly long initial travelling time therefore causing the birds to stay too long in their first visits. In addition, since the experimental trials only lasted 10 mins, Ollason argued that his model would not have time to fully equilibriate and therefore one would expect the birds to be staying too long even at the end of a trial. This is a more or less plausible argument, but apart from stating it in words, Ollason makes no attempt to develop it in any rigorous way. He does not model the effects of a 2 hr travelling time or make any predictions about how long it would take his model to equilibriate. He does not test his assumption that birds cannot tell the difference between a pretrial deprivation period and a within-trial travelling time. He does not test his assumption that great tits cannot learn that a foraging trial only last ten minutes and that they cannot adjust their behaviour accordingly. In any case, Ollason's explanation is almost certainly wrong. Other data (Cowie 1979; Cowie and Krebs, 1979) show that the first visits to patches after a period of deprivation were often shorter than subsequent visits. The point here is merely that over-protectiveness towards one's models is not exclusively a failing of optimal foraging theorists.

Optimal foraging theory is a natural extension of neo-Darwinism. From Darwin we arrive at the proposition that evolution will favour those individuals which maximise their reproductive fitness. Every activity in which an animal engages will have a bearing on that fitness, some in

obvious, others in unexpected ways. Using functional premises we can make informed guesses about what behaviours under which circumstances will contribute or detract from fitness. Optimal foraging theory enables us to make precise quantitative predictions against which to test our intuitions of what constitute the important elements of food seeking behaviour in a given situation.

Some predictions are banal. We expect animals to choose rich patches in preference to poor ones, for example. Yet even obvious predictions may not fully be borne out. Animals will often to continue to spend small amounts of time in patches which they "know" to be poor. Ollason might view this as evidence of the futility of optimality theories. Others might ask themselves if this seemingly wasteful behaviour could serve some worthwhile function. It could be construed as "sampling" behaviour, a way for the animal to make sure that the environment hasn't changed, that the poor patch hasn't become richer overnight. This is an *ad hoc* explanation but one that is testable. We may even re-employ optimal foraging theory to predict the conditions under which sampling behaviour will pay off and we can ask how long it should last (see Krebs et al., 1978; Houston et al., 1982). This is one example of the way in which the failure of animals to meet the optimal standards may stimulate fruitful research into functions of foraging behaviour that had previously been overlooked.

Another example was discussed in chapter 3. If we assume that animals are trying to maximise their rate of food intake then, in an environment of different prey types, the inclusion of poor types (e.g. ones with long handling times) in the diet depends upon the abundance of the better types. As the abundance of preferred prey decreases, so poorer prey should be eaten when encountered. Strictly speaking, the inclusion of lower ranking prey should occur in a step-like fashion. Thus the none of the No. 2 ranked prey should be eaten until the density of preferred prey has fallen below some critical threshold, at which point they should always be eaten whenver they are encountered. Similarly no prey ranked 3 or more should be included until the density of No.2 prey has fallen below some threshold. This foraging strategy ensures that poor prey are eaten only when doing so can increase feeding rate. However, empirical experiments (e.g. Lea, 1979) usually find that poorer items are included in *gradually* greater numbers as food abundance decreases. Animals thus show *partial* rather than the absolute preferences predicted by the rate maximising model. Once again one can conclude that optimal foraging theory has failed

to predict a real outcome. Or one can investigate further the nature of partial preferences. Several authors are following this path. Getty and Krebs (1985) argue that partial preferences occur because of the difficulties inherent in distinguishing good and bad prey. They use signal detection theory to show that great tits are slow to recognise changes in food abundance and hence make sub-optimal choices. Rechten et al. (1983) also use signal detection theory to test the misidentification hypothesis and conclude that it does not provide a full explanation (the birds' satiation level needs to be taken into account). Stephens (1985) is sure that the whole subject is a red herring and that partial preferences would be expected on purely statistical grounds. The question is by no means resolved but the debate is a healthy one which owes its existence to optimal foraging theory.

In some cases optimal foraging theory makes surprising predictions. That animals should be more ready to take risks when their energy reserves are low is not a strikingly obvious proposition. Yet this was a deduction which Caraco (1980) made on functional grounds and which he has since confirmed empirically, at least to his own satisfaction (Caraco et al., 1980). One may be critical of his method but the hypothesis is interesting and worth testing.

It is clear that, whether or not the predictions of optimal foraging theory are upheld, it has generated much interesting and worthwhile data. It might be argued that other theories would have given rise to more interesting and more worthwhile results. The concept of "satisficing" behaviour, mentioned at the beginning of this chapter, might be such a candidate. The concept was first mooted by Herbert Simon in 1956, and although it is often mentioned as an alternative to optimal foraging theory, it has not spawned many experimental tests (McCleery, 1979). It is worth considering why.

Simon's original model was of a hypothetical animal searching for food heaps scarcely distributed across a flat surface. He showed that an animal with limited vision did a lot better (880 times better in fact) than a blind animal which was obliged to forage randomly. Simon deliberately did not set his model animal a maximisation problem. "It needs only to maintain a certain average rate of food intake, and additional food is no use to it." He concluded that the possession of crude perceptual powers assured animals in his environment of "a high probability of survival over extended periods of time." Exactly how Simon's extended period of time

relates to an evolutionary time scale is not clear. Nor is it clear how one would go about testing an animals tendency to satisifice.

An advantage of optimality theories is that given basic assumptions about the environment and the function to be maximised, they generate precise quantitative predictions about animal behaviour. If, on the other hand, one expects an animal in a given environment merely to do enough to get by, then any behaviour that is better than random and worse than perfection will confirm one's expectation. It is hard to imagine any very rigorous definition of "doing enough to get by." A concept that is not susceptible to definition is not susceptible to experiment.

In addition, Dawkins (1982) notes that "Living things are not selected for their capacity simply to stay alive; they are staying alive in competition with other such living things." Optimal foraging theorists may argue that evolution favours those individuals which are better adapted to their environment, and that over many generations individuals will tend to behave close to the optimum. The extreme expression of this argument is "the empty assertion that what exists must be optimal" (McCleery, 1979). In reality there will always be constraints on perfect adaptation. We ought not to be surprised that animals do not maximise simplistic functions like rate of energy intake; their lives are more complicated than that.

Dawkins suggests the concept of "meliorizing" (from *melior* meaning better) as a happy compromise between satisficing and optimising (from *optimus* meaning best). (See also, Herrnstein and Vaughan, 1980, for an application of the same concept to animal learning.)

> Nature does not have the foresight to put together a sequence of mutations which, for all that they may entail temporary disadvantage, set a lineage on the road to ultimate global superiority. It cannot refrain from favouring slightly advantageous available mutations now, so as to take better advantage of superior mutations which may arrive later. Like a river, natural selection blindly meliorizes its way down successive lines of immediately available least resistance. The animal that results is not the most perfect design conceivable, nor is it merely good enough to scrape by. It is the product of a historical sequence of changes, each one of which represented, at best, the *better* of the alternatives that happened to be around at the time. (1982, p.46)

The trouble with meliorizing is that, like satisficing, it is doesn't give us any precise way of testing its validity. Returning to the problem posed at the beginning of this chapter, suppose we find an animal which fails to maximise its rate of energy intake. We may hypothesise that it is behaving optimally though maximising some other function; or that it is not perfectly adapted to its environment but doing the best it can given

evolutionary constraints; or that it is merely doing enough to get by. How does one distinguish between a performance that is genuinely sub-optimal and one that only appears to be sub-optimal because we have failed to pinpoint the correct function? How does one distinguish between the performance of an animal which uses a simple, general foraging rule that is robust over a wide range of circumstances, and that of an animal which is using a finely tuned rule that takes account of a wide variety of information, balances a wide variety of costs and benefits, and produces behaviour that is genuinely optimal in a general sense but fails in the narrow sense of maximising rate of energy intake? In what sense is the crude robust rule genuinely inferior to a subtle and complex rule? The latter may give a better feeding rate yet entail hidden costs -- the maintenance of a large brain for example.

Any attempt to categorise a performance as an example of optimising, meliorizing or satisficing will soon become bogged down by these questions. But we need not be despondent. The category in which one places an activity is less important than the mechanism which lies behind that activity. Regardless of one's bias towards optimising or satisficing, there are common problems to be tackled. We need to know what information animal's make use of and how they use it in their foraging decisions. Optimal foraging theory is useful as a heuristic device by which we may convince ourselves that we and our experimental subjects agree about the things that are important in foraging behaviour. If we believe that rate of energy intake is important we can use the theory to make statements such as "the best feeding rate in this environment can be achieved by behaving in the following way." If an animal comes close to the optimum we can build into our model a sensitivity to intake rate and begin to ask how the animal assesses it.

Theorists of all persuasions must eventually come up with concrete causal models of the behaviour that interests them. A good model is one which gives a good fit to the observed behaviour and one whose assumptions have independent support. The more specific the model, the more specific and testable will be its predictions.

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