BioOne COMPLETE

Optimal Foraging, Predation Risk and Territory Defence

Author: Krebs, J. R.

Source: Ardea, 55(1–2) : 83-90

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/arde.v68.p83

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

OPTIMAL FORAGING, PREDATION RISK AND TERRITORY DEFENCE

J. R. KREBS

Edward Grey Institute of Field Ornithology, Oxford OX1 3PS

CONTENTS

1. Introduction 83
2. Optimal diets, cryptic prey and predation risk 83
2.1. Cryptic prey 83
2.2. Predation risk 85
3. Switching between patches and territorial defence 87
4. Conclusions 89
5. Acknowledgements 90
6. Summary 90
7. References 90

1. INTRODUCTION

How do animals trade off feeding efficiency and predation risk? How does the need for territorial defence modify foraging behaviour? I will describe some preliminary attempts to look at specific examples of these problems in laboratory experiments with Great Tits (*Parus major*). The aim of these studies is to extend the ideas of simple optimal foraging models to include fitness costs associated with a variety of activities other than feeding. Traditional optimal foraging models (reviewed by Krebs 1978), which should perhaps be called "intake maximising" models, focussed only on the benefits of food intake. Such models use the hypothesis that animals forage so as to maximise the net rate of food intake, and formulate decision rules on this basis. More recently, a start has been made in examining how the risk of attack by predators might modify foraging behaviour (Milinski & Heller 1978), and in a more general context how time budgets and behaviour sequences are influenced by conflicting costs and benefits (McCleery 1978, Pulliam 1976, 1980).

In the first section of the paper I will describe an experimental test of a model for optimal choice of prey items which is based on intake maximising: the results are in qualitative agreement with the model, and I will argue that one aspect of the birds' behaviour which is not predicted by the model may be related to predation risk. The second section describes how the exploitation of patchily distributed food is modified when travelling between patches is associated with the opportunity for territorial defence.

2. OPTIMAL DIETS, CRYPTIC PREY AND PREDATION RISK

2.1. CRYPTIC PREY

The optimal diet model devised by Charnov (1976), McArthur (1972) and others predicts how a predator should choose between an array of prey types of different profitabilities. Profitability (or "prey value" Pulliam this symposium) is defined as the net food yield (E) per unit handling time (h). The model predicts that when a predator encounters profitable prey at a high rate, less profitable types will be omitted from the diet. This qualitative prediction has been substantiated in a number of field studies and laboratory experiments (Pulliam this symposium, Krebs 1978, Lea 1979). If the profitabilities of all prey types and their encounter rates are measured, an exact quantitative prediction can be made (Krebs *et al.* 1977). This prediction refers to whether or not a particular type of prey should be included in the diet.

Fig. 1 illustrates the idea for a simple example with two prey types. The predator's rate of intake if it eats only the more profitable type can be represented by the solid line. The axes of the graph are intake and time, so the slope of the line is the rate of intake. The prey values (E/h) of the profitable and unprofitable prey can be plotted on the same axes and are shown as dotted and broken lines respectively. The difference in slope between the dotted and solid lines represents the time taken to search for profitable prey. If the search time was zero the two lines would coincide. As the search time for profitable prey increases, the solid line decreases in slope (rotates clockwise) and when the search time is long enough for the solid line to have a shallower slope than the broken one, it will pay to eat both prey types. However, as long as the solid line has

Downloaded From: https://bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

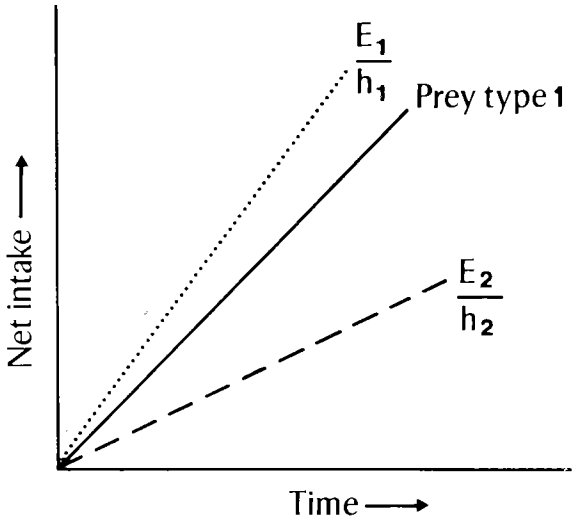


Fig. 1. A graphical representation of an optimal diet model. For explanation see text (after Krebs 1978).

a steeper slope than the broken one it will never pay to take the less profitable prey, regardless of their abundance. This is because any time taken off searching for and handling the first prey to handle the less profitable type will lower the slope of the solid line. The more time the predator spends handling the second prey, the closer the solid line will be "pulled down" towards the broken line. By a similar argument it will never pay to specialise on the less profitable prey. The best rate of intake that could be achieved by doing this is given by the broken line. Since the dotted line lies above this, it will always pay to spend time handling a more profitable item when it is encountered.

This model can be slightly modified to include the effects of crypsis (Charnov 1973, Hughes 1979, Erichsen *et al.* 1980) by considering that crypsis imposes a cost on the predator in the form of a "discrimination time": the time needed to distinguish the prey item from its background. Each time the predator eats a cryptic item, it pays the time cost of both handling and discrimination. The way in which this changes the predictions of the model can be illustrated by again referring to the example with two prey types; profitable and unprofitable. If only the profitable prey are cryptic, a predator specializing on this type (as in Fig. 1) will pay the discrimination cost, while one which eats only conspicuous unprofitable prey will not. One can see, therefore, that if the discrimination cost is sufficiently high, the predator may do better by switching to the second prey. In effect, crypsis has lowered the profitability of the first prey by increasing the handling time. Thus the model with crypsis could predict switching back and forth between prey types as the degree of crypsis changes.

Erichsen *et al.* (1980) tested this model using captive Great Tits feeding off a conveyor belt attached to the front of a cage (Krebs *et al.* 1977). The advantage of this set up, in which the prey move past the bird rather than vice-versa, is that the encounter rate with different prey types can be precisely controlled, and held constant throughout an experiment by replenishing the prey on the belt. The birds were presented with two prey types: cryptic, profitable and conspicuous, unprofitable prey. The profitable prey, which consisted of large pieces of mealworm (*Tenebrio* species) inside opaque plastic straws, were cryptic because they resembled very closely "twigs", which were straws containing string instead of a worm. This kind of crypsis is called "special protective resemblance" (Cott 1940). The unprofitable prey were small worms inside clear plastic straws. The birds handled prey by picking them off the belt, flying to a nearby perch, and extracting the worm with the beak while holding the straw under one foot. The degree of crypsis of the profitable prey was varied by altering the ratio of worms to twigs in opaque straws encountered by the birds, and the discrimination time was measured as the time taken to pick up and reject a twig, fly to the perch, look into the straw and drop it.

Fig. 2 shows the results of an experiment in which there were two treatments. In treatment A, the ratio of twigs to profitable worms was high enough to predict that the birds would specialize on unprofitable prey, which they did. In the second treatment both the prediction and the birds' behaviour was reversed (Erichsen *et al.* 1980). It is also worth noting that the model with no discrimination time (Fig. 1) makes exactly the opposite prediction (that the birds should specialize on profitable worms) for treatment A.

While the results are in qualitative agreement

Downloaded From: https://bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

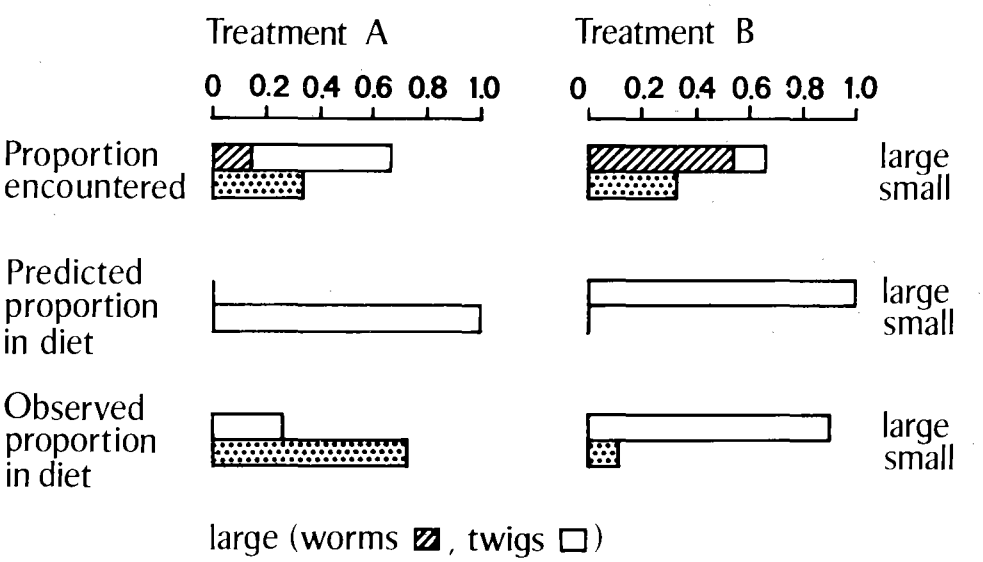


Fig. 2. The results of an experiment on prey selection. As predicted, the birds switched from specialising on the less profitable but more conspicuous of the prey types in treatment A, to specialising on profitable cryptic items in B. The difference between treatments was in the ratio of profitable prey to "twigs" encountered. The profitable prey mimicked inedible twigs. The results are the mean values of five birds. For details see Erichsen *et al.* (1980).

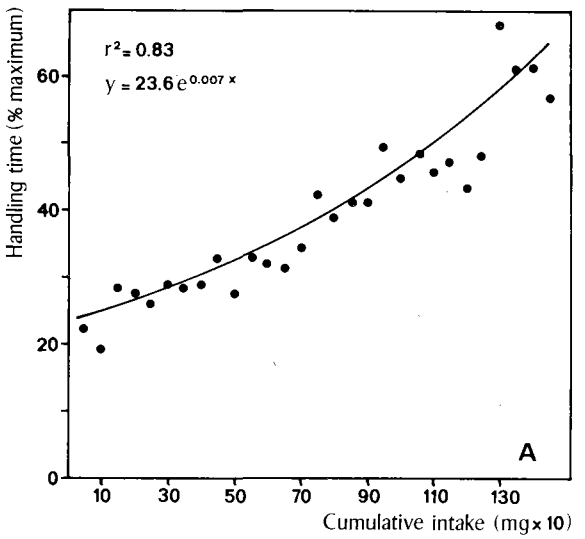
with the model, the quantitative predictions are wrong. First, as shown in Fig. 2, the switch from specializing on unprofitable to profitable prey was not an all-or-nothing change. This is possible because the model is deterministic. A probabilistic analogue (which is certain to be more realistic since the animal never has perfect knowledge) might be able to predict the incomplete switch. The second discrepancy is that handling time is not, as assumed by the model, a constant: it varies systematically with the level of food deprivation of the birds (Fig. 3). The same effect is known for other species (Werner 1974, Zach & Falls 1978) and has been previously observed in the Great Tit (Smith & Dawkins 1971). I will argue that the change in handling time with hunger is a result of the tradeoff between maximising feeding rate and mimimising predation risk, and that it is part of a general slowing down of feeding rate as animals approach satiation (McCleery 1978).

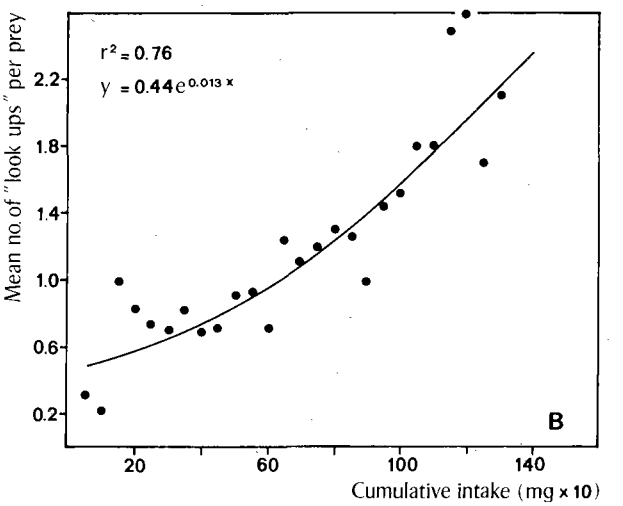
2.2. PREDATION RISK

A detailed analysis of the behaviour of Great Tits while handling prey items shows that the exponential increase in handling time as the bird approaches satiation (Fig. 3A) is in a large part due to an increase in the time spent "looking up" during handling (Cowie *et al.* in prep.). The birds handles each item by holding it under one foot and pecking at it. This rapid pecking and swallowing is interrupted by occassional periods of lifting the head above horizontal and scanning rapidly from side to side. Looking up is often assumed to be a form of scanning for predators (see also Pulliam, this symposium). Experiments with birds deprived of food for different lengths of time show that the relationship between looking up and hunger (Fig. 3B) is direct, and not a consequence of changes in behaviour related to the time since start of a trial. Fig. 3C shows that the interprey waiting time also increases exponentially towards satiation, thus the change in handling time can be seen as part of a gradual decrease in feeding rate. The data can also be plotted as a "satiation curve" of cumulative intake as a function of time as can be seen in Fig. 4 (McCleery 1978).

McCleery (1978) has proposed a functional explanation for satiation curves. He suggests that the cost of being hungry (risk of death due to starvation) is related to deficit by an accelerating curve: a slight extra deficit when the animal is nearly satiated results in a very small increase in

Downloaded From: https://bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use





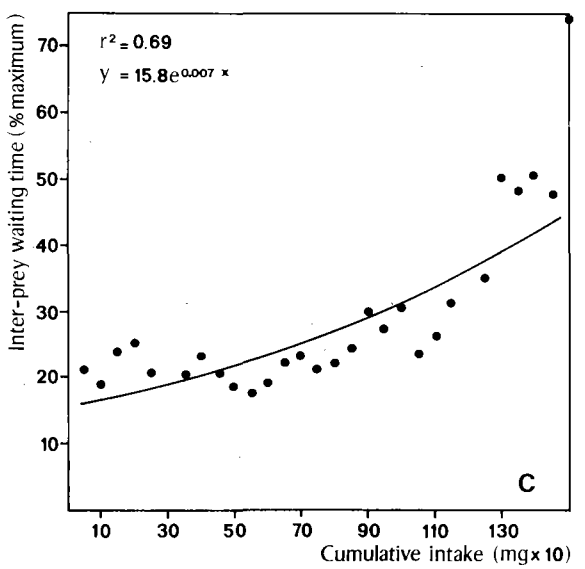


Fig. 3. A-C The results of an experiment in which five Great Tits were deprived of food overnight at room temperature and allowed to eat mealworm pieces until satiated. Handling time, looking up and interprey interval increased exponentially as the birds approach satiation.

risk, but a similar increment in deficit when the animal is near starvation greatly increases the risk of death. Similarly, it can be argued that there is a cost associated with feeding, and that this cost increases at an accelerating rate as the rate of feeding increases. This argument applies whether the rate-dependent cost is primarily energetic (a doubling of running speed more than doubles the energy cost) or is dependent on excluding other activities (while it is easy to walk and talk at the same time, it is hard to run and talk). The cost of rapid handling of prey and feeding rapidly in the Great Tit is more likely to be of the second kind than of the first: since rapid handling is associated with low rates of looking up, the rate-dependent cost of feeding is likely to be lack of vigilance for predators.

In summary, satiation curves can be explained by postulating that a very hungry animal has a high deficit cost and is therefore willing to pay a high feeding rate cost to reduce its deficit, while a nearly satiated animal will be prepared to pay only a low feeding cost. In the particular case of the Great Tit, the hypothesis is that a hungry bird will tolerate a high risk of predation to decrease its deficit, while a less hungry bird attends more to predators and less to decreasing its deficit.

This verbal argument can be made more rigorous in the form of an optimisation model which predicts the feeding rate for a given deficit and specified costs associated with feeding rate (Milinski & Heller 1978). The model, in contrast to traditional static optimal foraging models is a dynamic one, in which the animal's behaviour results in changes in its state. McCleery (1978) shows that exponential satiation curves of the type shown in Fig. 4 would arise of both the deficit cost and costs related to feeding rate are of a quadratic form.

If, as surmised above, the change in handling

Downloaded From: https://bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

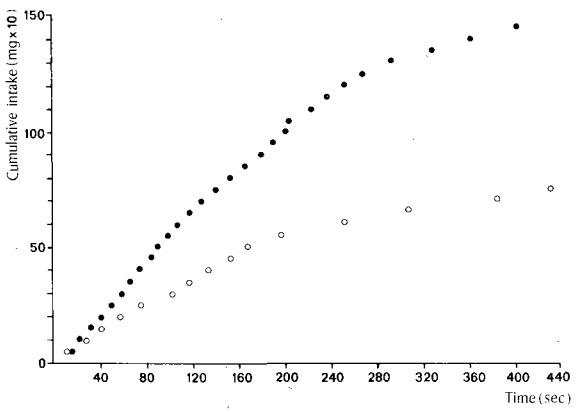


Fig. 4. The data of Fig. 3 A-C can be plotted as satiation curves: examples for two birds are shown and the other individuals gave similar results.

time of Great Tits is related to predator vigilance, it should be possible to increase the handling time and frequency of looking up in hungry birds by exposing them to a high risk of predation (Milinski & Heller 1978). Cowie *et al.* (in prep.) describe an attempt to do this by exposing food-deprived Great Tits to a view of a stuffed Sparrowhawk, or a control object, for 10 sec just before allowing them to start feeding on mealworms in the conveyor belt apparatus described earlier. Although there were difficulties in carrying out the experiment (because the effect of exposure to the predator may have lasted over several trials), the results showed that handling time, looking up rate, and interprey waiting time increase in hungry birds when they had just been exposed to the hawk. It appears that when the birds assess the risk of predation as being high, fast feeding is compromised for greater vigilance, which supports the original hypothesis that handling time is a tradeoff between vigilance and feeding.

3. SWITCHING BETWEEN PATCHES AND TERRITORIAL DEFENCE

The marginal value model (Charnov 1976) is perhaps the most thoroughly tested of the traditional optimal foraging models (Krebs *et al.* 1980). The model predicts, on the basis of maximising intake as the optimality criterion, how long a predator should spend in a patch of food which is gradually depleted. If the depletion curve of prey within a patch and the average time taken by the predator to travel between patches are both measured, the model can be tested using a graphical solution (Cowie 1977, Parker & Stuart 1976).

Using Great Tits searching for mealworms hidden in sawdust-filled plastic pots (patches) in a large aviary, Cowie (1977) showed that the model was successful in predicting the relationship between average travel time and average time spent in a patch. When the travel time was experimentally increased, the time spent in each patch increased by the predicted amount.

Travelling between patches has costs other than time, for example the energetic costs or increased risk of predation while flying between bushes, and Cowie (1977) showed that when energetic costs of flying are taken into account, the model gave a more accurate prediction of the birds' behaviour. Fig. 5 illustrates graphically how the costs or benefits associated with travelling alter the predicted time spent in each patch; if some kind of benefit accrues while travelling, the time spent in a patch should be shorter.

Kacelnik (1979) describes an experiment in which there is a benefit of travelling between patches associated with territorial defence. The experimental arrangement is shown in Fig. 6. Two male Great Tits lived in the two outdoor aviaries in visual isolation, and on alternate days each individual was allowed into the indoor aviary where it foraged in two "patches". Thus both birds behaved as though the whole aviary was within their territory, although they did not normally come into contact. The "patches" consisted of operant devices similar to those used by Krebs *et al.* (1978), in which the birds could work for food by hopping on a perch to deliver a food item (pupa of *Calliphora* species). Each patch was programmed to operate in such a way that the longer a bird stayed in one patch, the more hops were required to earn the next prey item. When the bird switched to the other patch, the "depleted" one was re-set, so that by switching at the appropriate moment the bird could maximise its intake rate according to the marginal value model (Fig. 5a). The two patches were hidden behind vertical screens, so that the foraging bird

Downloaded From: https://bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

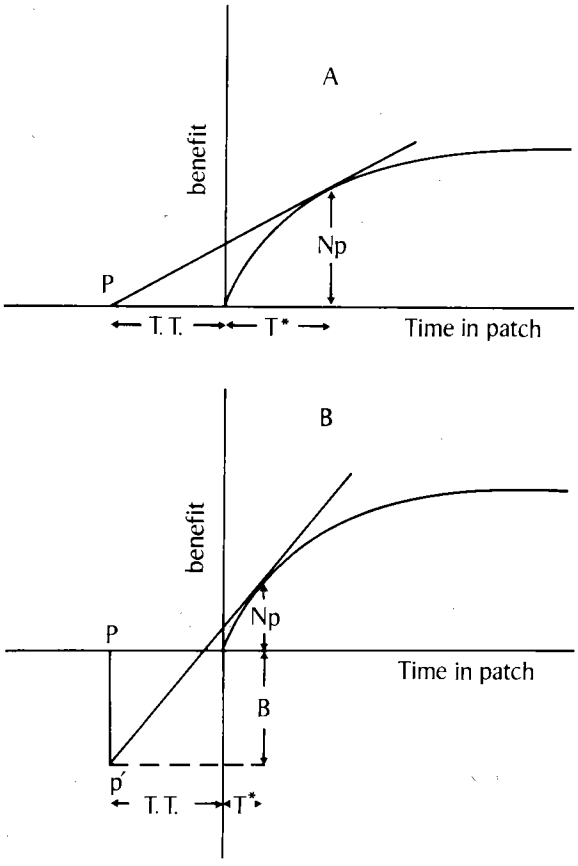


Fig. 5. Calculation of the territorial benefit required to change the patch time by a given amount. The method is based on the graph presented by Cowie (1977).
A. No benefit associated with travelling between patches: N_p = optimal no. of prey eaten per patch; T* = optimal time in patch; T.T. = travel time; P = point of origin on abscissa of tangent used to find optimal values of N_p and T.
B. A benefit B is obtained while travelling between patches. The tangent to find the optimal values of N_p and T is now traced from a new origin P' situated B units below P. When the change in N_p but not the value of B is known (as in the experiments described in the text), B can be calculated using an inverse optimality procedure (after Kacelnik 1979).

did not have a view of the whole aviary, and especially of the "intrusion boxes". These boxes were used to set up territorial intrusions as follows. One of the two birds (the experimental individual for that session) was allowed into the indoor aviary to forage; and the second bird was trapped in the intrusion box. The box normally acted as a short passageway through which the birds passed from the outside to the inside aviary, but during an intrusion the intruder was held in the box with two sliding screens, the one facing the indoor aviary being made of transparent plexiglass. The aim of the experiment was to compare the switching of the experimental bird between patches in control conditions with no intrusion, and after a brief exposure to an intrusion just before starting to forage. The benefit associated with travelling between patches in the latter treatment is that the flying bird could inspect the intrusion box, whereas it could not do so while foraging. The prediction was that the time spent in a patch before switching should be as expected from the marginal value model in control conditions, and shorter than this in the experimental conditions, where the birds should adopt a compromise between territorial vigilance and foraging efficiency (Fig. 5).

Kacelnik (1979) tested four males in this experiment and found that three of the four behaved approximately as predicted. Although there was a considerable spread of visit lengths, the modal length of visit to a patch was as predicted by the marginal value model in three birds during control conditions, and there was a shift by those individuals towards shorter visits in the experimental treatments. It is possible to work out how much an individual would lose in terms of rate of

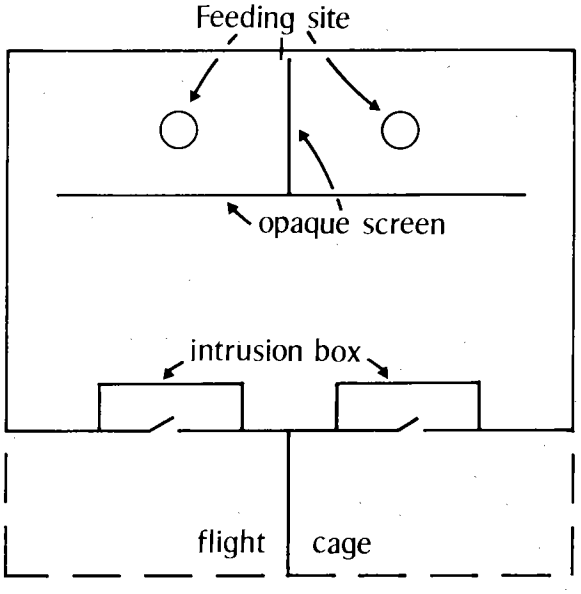


Fig. 6. The experimental set-up by Kacelnik (1979) to study the trade-off between foraging and territorial defence.

Downloaded From: https://bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

food intake by decreasing its visit length in the experimental treatment. This value depends on individual constraints of travel time, hopping rate and so on. It is interesting to note that the individual which failed to show a change in patch time in the experimental condition is the one which would have lost most in terms of rate of food intake by so doing (Kacelnik 1979).

4. CONCLUSIONS

The experiments on handling time and time spent in patches suggest that Great Tits can modify their foraging behaviour to trade off feeding efficiency with predation risk or territorial defence. The results are qualitatively as predicted, but is it possible to make more quantitative statements about the trade off? The answer depends on whether or not it is possible to calibrate the benefit of feeding against benefits from territory defence or predator avoidance. Once the problem of calibration has been solved, a common currency can be used to predict the exact optimal balance between different kinds of activity (McFarland 1976). One approach to this problem is to use time as a common currency (Davies, Pulliam, this symposium). For example in Davies' study of Pied Wagtail territoriality, the cost of territorial defence was measured purely in time lost from foraging, so that the optimal policy (exclusion versus tolerance of satellites) was simply the one which maximised net rate of food intake. There may be other costs associated with territorial defence such as predation or injury risk, but these do not seem to be important in Pied Wagtails. However, in the experiments with Great Tits which I have described the birds clearly do not maximise net rate of intake, so that the calibration problem cannot be treated as one in which time is the common currency, and vigilance, for example, operates as a time constraint. A second way of solving the calibration problem would be to measure directly in the field the costs associated with different activities, for example the risk per unit time of death from predation while feeding at a certain rate, or the risk per unit time of losing a territory through lack of vigilance. This is not usually a feasible proposition, although some studies have made a start in this direction (McFarland 1977). The third method is to treat the animals' behaviour as an estimate of the calibration. As McFarland (1976) has argued, if the animal has been designed by natural selection to calibrate different costs against one another, its decision rules should reflect the relevant calibration. One example of this kind of approach was referred to in the experiment on the tradeoff between foraging and territory defence. The benefit derived from patrolling the territory while travelling between patches could be expressed in terms of prey units. As a result of increasing its rate of switching between patches, a bird decreased its rate of intake from the maximum attainable, and the decrease could be considered as the bird's estimate of the benefit of territorial vigilance relative to feeding. A more ambitious application of the same rationale is illustrated by the discussion of predation risk and handling time. As pointed out earlier, the exponential decrease in feeding rate as the birds approached satiation is consistent with a model in which the costs associated with hunger and variation in feeding rate (anti-predator vigilance) are quadratic in form (McCleery 1978). Thus one could argue that the experiments suggest an exact form of a combined cost function for feeding and predation. This cost function could be used to make further quantitative predictions about the trade-off between foraging and predation risk. One problem is that of exclusivity: there may be alternative cost functions which give a similar prediction of exponential satiation. Thus all the methods have difficulties, and probably the most fruitful approach will be a combination of assessing costs directly where possible to test inferences drawn from observing decision rules in experimental studies.

A second general point raised by the experiments I have described is that of constraints. Any optimisation model contains assumptions about constraints on the animal's performance (Sibly & McFarland 1976, Maynard Smith 1978), and in fact one of the purposes of building optimality models is to help to understand the constraints which are operating in a particular case (Maynard Smith 1978). The optimal diet model described at the beginning of this paper assumed that handling time is a constraint, while more de-

Downloaded From: https://bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

tailed observations showed that this is in fact not true, since handling time varies with hunger level. Similarly, discrimination time which was treated as a fixed constraint, may be modifiable through experience (Dawkins 1971), and this can be incorporated into an optimal diet model (Hughes 1979). In general, it might turn out many behavioural attributes which are treated as fixed constraints in simple optimal foraging models are actually variably, and can be altered according to environmental risks.

5. ACKNOWLEDGEMENTS

I thank the S.R.C. for financial support and Chris Perrins for his comments on the manuscript.

6. SUMMARY

Optimal foraging models can be extended to include tradeoffs competing activities. I describe two examples in which Great Tits apparently reach a compromise between maximising rate of food intake and vigilance for predators or vigilance for territorial intrusions.

The results of the experiments are qualitatively as expected from optimality considerations but it is necessary to calibrate feeding benefit against risk from predation or territorial intrusion before quantitative predictions can be made. I discuss ways of obtaining such a calibration.

7. REFERENCES

Charnov, E. L. 1973. Optimal foraging: some theoretical explorations. Ph. D. thesis. University of Washington.

Charnov, E. L. 1976. Optimal foraging: the attack strategy. Am. Nat. 110: 141—157.

Cott, H. B. 1940. Adaptive coloration in animals. London, Methuen.

Cowie, R. J. 1977. Optimal foraging in Great Tits (*Parus major*) Nature 268: 137—139.

Dawkins, M. 1971. Perceptual changes in chicks, another look at the "search image" concept. Anim. Behav. 19: 566—574.

Erichsen, J. T., J. R. Krebs & A. J. Houston. 1980. Optimal foraging and cryptic prey. J. Anim. Ecol. 49: 271—276.

Hughes, R. N. 1979. Optimal diets and the energy maximisation premise: the effects of recognition time and learning. Am. Nat. 113: 209—221.

Kacelnik, A. 1979. Studies of time budgets and foraging behaviour in Great Tits. D. Phil. thesis. Oxford.

Krebs, J. R. 1978. Optimal foraging: decision rules for predators. Ch. 2 in: J. R. Krebs & N. B. Davies (eds.). Behavioural Ecology: and evolutionary approach. Blackwell Scientific Publications, Oxford.

Krebs, J. R., J. T. Erichsen, M. I. Webber & E. L. Charnov. 1977. Optimal prey selection in the Great Tit (*Parus major*) Anim. Behav. 25: 30—38.

Krebs, J. R., A. I. Houston & E. L. Charnov. 1980. Recent developments in optimal foraging. In: A. C. Kamil & T. D. Sargent (eds.). Mechanisms of foraging behaviour. Garland Press.

Krebs, J. R., A. Kacelnik & P. J. Taylor. 1978. Test of optimal sampling by foraging Great Tits. Nature 275: 27—31.

Lea, S. E. G. 1979. Foraging and reinforcement schedules in the pigeon: optimal and non-optimal aspects of choice. Anim. Behav. 27: 875—886.

McArthur, R. H. 1972. Geographical Ecology. Harper and Row N.Y.

McCleery, R. H. 1978. Optimal behaviour sequences and decision making. Ch. 13 in: J. R. Krebs & N. B. Davies (eds.). Behavioural Ecology: an evolutionary approach. Blackwell Scientific Publications, Oxford.

McFarland, D. J. 1976. Form and function in animal behaviour. In: P. P. G. Bateson & R. A. Hinde (eds.). Growing points in ethology. Cambridge University Press. Cambridge.

McFarland, D. J. 1977. Decision making in animals. Nature 269: 15—21.

Maynard Smith, J. 1978. Optimisation theory in evolution. A Rev. Ecol. Syst. 9: 31—56.

Milinski, M. & R. Heller. 1978. The influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). Nature 275: 642—644.

Parker, G. A. & R. A. Stuart. 1976. Animal behaviour as a strategy optimiser: the evolution of resource assessment strategies and optimal emigration thresholds. Am. Nat. 110: 1055—1076.

Pulliam, H. R. 1976. The principle of optimal behaviour and the theory of communities. In: P. P. G. Bateson & P. H. Klopfer (eds.). Perspectives in Ethology Vol. 2 pp. 311—332. Plenum Press, N.Y.

Sibly, R. M. & D. J. McFarland. 1976. On the fitness of behaviour sequences. Am. Nat. 110: 601—617.

Smith, J. N. M. & R. Dawkins. 1971. The hunting behaviour of individual Great Tits in relation to spatial variations in their food density. Anim. Behav. 19: 695—706.

Werner, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Bd. Can. 31: 1531—1536.

Zach, R. & J. B. Falls. 1978. Prey selection by captive Ovenbirds (Aves: Parulidae) J. Anim. Ecol. 47: 929—943.

Downloaded From: https://bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use