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POPULATION DYNAMICS AND COST-BENEFIT ANALYSIS

AN ATTEMPT TO RELATE POPULATION DYNAMICS VIA LIFETIME REPRODUCTIVE SUCCESS TO SHORT-TERM DECISIONS

by

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SUMMARY

1. The aim of this article is to explore whether cost-benefit analysis of behaviour may help to understand the population dynamics of a species. The Great Tit is taken as an example.
2. The lifetime reproductive success in different populations of Great Tits amounts from 0.7 (Hoge Veluwe, Wytham) to 1.5 recruits per pair in an island population (Vlieland). As numbers stay roughly stable the difference points at dispersal as an important factor determining local recruitment.
3. The variation in lifetime reproductive success between individuals can be explained in the first place by variations in the recruitment rate, the chance that a fledgling returns as a breeding bird. Also variations in lifespan play a role in determining variations in lifetime reproductive success. Variations in beech crop index are not responsible for these effects.
4. Juvenile Great Tits start competing for territories in autumn. Both the density of resident territorial males and the density of candidate males affect the probability that a candidate will get a territory. A descriptive model shows that the effect of the density of resident males on the candidate settling chance is always negative. However, the effect of candidate density is dependent on the density of resident males. At low resident male densities the density of candidates has a negative effect, and at high resident male densities a positive effect on settling chance of a candidate. The consequences of this model for the settling pattern in other woods under study are discussed.
5. A speculative cost-benefit model is developed in order to explain the interaction between resident male density and candidate density in explaining settling chance as mentioned under 4.
6. Experimental manipulation of brood size is undertaken in order to measure costs and benefits associated to brood size. On basis of these experiments an optimisation model is constructed that predicts the clutch size that maximizes first clutch recruitment. This is done on basis of a relation between manipulated brood size and nestling weight and a relation between nestling weight and recruitment probability. The prediction is far greater than the actual brood size.
7. The negative effect of an increase in brood size on the probability of producing a second clutch was included in the model, now predicting the maximal annual recruitment as a function of the size of the first brood. The predicted brood size shifts to a lower value close to the observed.
8. Measurements of energy content of female Great Tits in the incubation period in relation to temperature reveal a serious loss of fat reserves at low ambient temperatures. Whether these losses are also related to clutch size is not known.
9. The role that these models may play in understanding population dynamics is discussed.

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1. INTRODUCTION

Population studies investigate both the variations in numbers, the dynamics, and the average level of numbers over a longer period, the statics of populations. It is difficult to define a population in nature, as its definition is dependent on the behaviour of individuals (BAKKER, 1964). Population studies approach the problem by recording fluctuations in numbers within plots and deduce from the results general principles which are applied to larger populations.

Klomp always had a wide interest in population studies both as a theoretician and as a conservationist. He had a special interest in density dependence in animal populations and wanted to know whether such processes would lead to stabilization of animal numbers. For this goal he chose to work on the Pine Looper, *Bupalus piniarius*. However, he kept his interest in population studies of birds as demonstrated by two important review papers, one on clutch size (KLOMP, 1970) and the other on territoriality (KLOMP, 1972). Both are essential topics in order to understand density dependent processes in bird populations. Klomp took upon himself the task of writing a review paper on the population studies of the Great Tit (KLOMP, 1980), taking the opportunity to explain his view on how these ought to be done in the future. These three publications were used as a starting point to discuss some aspects of our work relevant to the problems that Klomp has always thought to be the main problems in the study of animal numbers.

Historically, there have been two important approaches to the Great Tit research in the Netherlands. The observation that popula-

tion densities in 'poor' habitats only increase when the density in the 'rich' habitat has reached a certain level (the 'buffer effect', KLUYVER & TINBERGEN, 1953) strongly emphasized the role of spatial processes. This finding has been central in the development of the theory on numbers and distribution. FRETWELL's (1972) 'ideal free distribution' is a more sophisticated version. As territoriality is one of the possible underlying spatial mechanisms detailed analysis of territorial behaviour was chosen as a follow up.

The other important line concerns the feeding ecology of the tits. In order to estimate the effect of Great Tit populations on their food supply TINBERGEN (1960) studied the diet of nestlings and the densities of their prey in great detail. Because the data were gathered at the individual level, these studies led to important theoretical ideas such as the 'search-image' hypothesis, and stimulated many scientists in different fields. However, the effect of the Great Tits on their prey populations was less pronounced than had been expected (KLUMP & TINBERGEN, 1960) and regulation of prey numbers was more likely to be brought about by parasites that are able to respond numerically to increases in their host populations (VAN ALPHEN, this volume). Nevertheless it was clear that the food supply played an important role in the ecology of the Great Tit and therefore VAN BALEN (1973) decided to follow up this aspect of the work. He started a research program to investigate the role of food in the observed differences in population characteristics between Great Tits in pine and oak woods. This resulted in a much better understanding of the role of food abundance in space and time in the determination of numbers.

Recently, detailed analyses of the costs and benefits, associated with different decisions individual animals may take, have greatly improved the understanding of decision processes in animal behaviour (DRENT & DAAN, 1980; MCCLEERY, 1978; MCFARLAND, 1977). Since both average levels and fluctuations in density originate in the behaviour of individual birds with regard to environment and conspecifics, we expect the cost benefit approach to be rewarding to population dynamics. The following is a report of work in progress on the costs and benefits of different behavioural choices partly using experimental methods. The aim of these tests is to trace which factors involve a cost and which a benefit to the individual under study and how these are associated with a particular decision it makes. Sound knowledge of cost and benefit functions will enable us to predict behaviour. Research into this aspect is of great importance to our understanding of animal behaviour in general and therefore to the understanding of the dynamics of populations.

The basis of our research is a long-term monitoring project in different types of woods started by Kluyver in 1955 and continued by Van Balen. The collected demographic data are used to detect main factors governing Great Tit numbers. Subsequently experiments were designed to test whether the observed correlations have causal components. The Great Tit is especially suited to population studies as it is sedentary, it can readily be caught and marked individually, the breeding biology can be registered in great detail as a consequence of the habit of breeding in nestboxes, and further manipulation within the nestbox is relatively easy. Further the large body of data available on individual birds over a series of years enables us to make a correlative analysis of their life histories. Moreover, in the long term, population properties may change due to selection pressures. This may cause shifts in the relative importance of different factors which may give insight into the flexibility of the mechanisms determining animal numbers.

As a starting point for this paper we have taken an analysis of the lifetime reproductive success (LRS) in two different areas. This was used to assess the components of LRS that vary most between individuals and thus primarily affect variations in lifetime reproductive output. This is followed by a discussion of two subjects: territoriality and reproduction. Both are more or less directly related to variations in recruitment rate and life span, the main factors emerging from the first analysis. In discussing our work we hope to show that the cost benefit approach is relevant to the study of animal numbers and that future research may develop along these lines, in part suggested by Klomp in his last review on Great Tit population dynamics.

2. LIFETIME REPRODUCTIVE SUCCESS

As stated in the introduction the analysis of population data may either concentrate on fluctuations in time, or alternatively it may emphasize average levels typical for a specific population. The analysis of lifetime reproductive success (LRS) as defined below belongs to the second category. Data over a long series of years were analysed, to gain insight into the lifetime reproduction of Great Tits, and to compare two of our populations.

A useful aspect of the analysis of the variation in LRS is that it can be broken down into components and that the contribution of each component to the total variation of the LRS can be quantified (CLUTTON-BROCK, 1987). We will discuss here some of the main results of a recent analysis published by VAN BALEN *et al.* (1987). Estimation of lifetime reproductive success in the field can only be

achieved if complete data on individual birds are available. The data of the long term population study of the Great Tit on Vlieland and in the Hoge Veluwe are suitable for this analysis. Virtually all the birds, both adults and nestlings, have been ringed in the Hoge Veluwe (VAN BALEN *et al.*, 1987) and the Vlieland population (KLUYVER, 1971; TINBERGEN *et al.*, 1985). The birds were ringed either as nestlings or as adults entering the population from outside. Each year a large proportion of birds are caught in the reproductive season and their breeding parameters measured. In this way we know the lifetime breeding history of individual birds (for details see VAN BALEN *et al.*, 1987).

The number of recruits per parent (LRS) can be estimated from the following five components:

1. Life span, defined as the number of observed reproductive years (LS).
2. The number of clutches per year (CY).
3. The number of eggs per clutch (EC).
4. The number of fledglings in relation to the number of eggs laid (FE)
5. The number of local recruits in relation to the number of fledglings (RF).

Lifetime reproductive success is defined as the product of these parameters:

$$\text{LRS} = \text{LS} \cdot \text{CY} \cdot \text{EC} \cdot \text{FE} \cdot \text{RF}.$$

As these estimates are based on measurements within a certain area they may be biased for dispersion.

The question is to what extent inter-individual variation in LRS can be attributed to variation in the components of this product. The answer gives an indication about the most important variables that explain the variation in LRS in a natural situation, and can focus our research effort on these important sources of variation.

The mean number of local recruits per female in her lifetime in the Hoge Veluwe area is only 0.8, and the variation between individuals is enormous. Fifty percent of the females produce all the recruits. The mean number of recruits per female is lower than one would expect in a stable population without migration, where each female should produce two recruits to replace herself and her mate. So without immigration numbers cannot be locally stable. This stresses the crucial role that dispersion must play in determining numbers, and it illustrates the problems in defining a population as stated in the introduction. For this reason it is particularly interesting to compare the Hoge Veluwe data to those collected on the island of Vlieland. DRENT (1984) showed that some of the dispersal of the yearling birds takes

place just after fledging. This early dispersal may lead to breeding outside the study plot on the mainland but, as on Vlieland the whole island is under study, it may not have the same consequences. However, dispersal in a later stage will occur both from the mainland and the island, be it possibly in different intensities. As expected the LRS on Vlieland is higher than in the Hoge Veluwe: 1.53 recruits per female per lifetime. This still does not equal the expected 2 for situations without immigration and with stable numbers. Even on Vlieland immigration plays a role in determining numbers, be it less pronounced than in the Hoge Veluwe. If we wish to explain local breeding densities we will have to study migration and especially the processes involved in the distribution of the fledglings in their first year. Computation of LRS is done on the basis of local recruitment and therefore should be regarded as local LRS. The possible effects of dispersion should always be borne in mind when interpreting the results.

BROWN (1987) developed a method to compute the role that the variances of the individual components of LRS play in explaining the variance in total LRS. For this purpose standardized variances of all components of LRS and LRS itself were computed. The analysis of partitioning of the variance reveals that variation in LRS is mainly due to variation in the local fledgling survival rate (RF). Life span (LS) and egg and nestling survival (FE) are the next largest single contributors to the variation in LRS (fig. 1). Analyses of the LRS of the males in our woods, as well as a comparable analysis of the population in Wytham Wood, U.K., (McCLEERY & PERRINS, 1987) give essentially the same results. Local LRS in Wytham Wood is 0.7 recruits per female.

In order to find out which factors cause these differences, VAN BALEN *et al.* (1987) analysed the LRS for particular cohorts selected on the basis of external factors, known to affect the annual recruitment rate, such as the beech crop index in the first winter. The same two factors (RF and LS) were the most important in explaining variations in lifetime reproductive success, indicating that variations in the beech crop in the first winter did not cause the observed pattern. Recently new methods of analysis have been developed which may help to disentangle the sources of variation at the different levels (CLOBERT *et al.*, 1985, 1987).

Concluding we can say that recruitment rate and to a lesser extent life span of the adults are two factors that explain a large part of the variation in lifetime reproductive success. The central question now becomes: what factors are important in determining the variation in RF and LS. Basically the variations can be the result of differences

Fig. 1. The percentage of variance in LRS of females that can be explained by first order contributions of variance in the components of LRS for the Hoge Veluwe (1973-1981, $n = 553$) and Vlieland (1975-1981, $n = 323$). As higher order contributions are not given, the sum of the explained variance may exceed one hundred per cent.

between years, between cohorts, between individuals and between local environmental factors. There is extensive knowledge of the factors that determine annual variation in adult and juvenile survival (PERRINS, 1965; VAN BALEN, 1980; TINBERGEN *et al.*, 1985). However, more knowledge of the selection pressures at work in the fledglings first year is needed, to unravel which properties of individuals may lead to a high survival rate.

3. AUTUMN TERRITORIALITY

3.1 Introduction

The annual local survival rate of fledgling is often negatively affected by the Great Tit density (PERRINS, 1979; DHONDT, 1971; VAN BALEN, 1980; TINBERGEN *et al.*, 1985). This density dependence has received a lot of attention since it can stabilize animal numbers. The underlying mechanisms however are poorly understood. Both competition for space (KLUYVER, 1951, 1971) and competition for food (LACK, 1954, 1966) have been advanced, but critical data are lacking, partly because food and space are so closely related. In his review on territoriality KLOMP (1972) states that 'direct observations and removal experiments are indispensable for giving the final proof'.

Work by DHONDT & HUBLÉ (1968), DHONDT (1971) and KREBS (1971) had already shown that characteristics of the territory may differ considerably for individuals, areas and years, but the relationship between territoriality and population size was often not studied in detail. In more recent years extensive work has been done on the economics of territoriality (Davies, 1980; DAVIES & HOUSTON, 1981; GILL & WOLF, 1975; PYKE, 1979). This work has concentrated on those situations where territories are very flexible and quickly adjusted to local situations, emphasizing short-term benefits and costs. Longer term costs and benefits must be important but are harder to study.

DRENT (1983) started a study on the territoriality of the Great Tit with basically two aims. Firstly he wanted to describe the behaviour of juvenile males in order to trace the development of agonistic behaviour, leading finally to territoriality. Secondly he wanted to estimate in different habitats the effects of territoriality on reproduction and survival chances of individual birds and consequently on the population as a whole.

KLUYVER & TINBERGEN (1953), BROWN (1969) and FRETWELL & LUCAS (1970) have developed models of settlement in non-homogeneous habitats. Brown models the situation in which the settlers occupy a territory with fixed size and settle in the best habitat. Fretwell and Lucas were primarily concerned with the occupation of habitats of different quality. KLUYVER (1951), and DRENT (1983) state that young male Great Tits try to occupy territories well before the start of winter and adult males have to defend their territories against these candidates. This means that birds of different status are involved in the competition for territories. Drent's approach has been to measure carefully the density of potential settlers and the density of adult territorial males and score the number of the potential settlers that actually succeed in obtaining a territory. Subsequently, a descriptive model was formulated and tested with new data and experiments. The relevance of this descriptive model to density dependence for woods with different densities of adult males and potential settlers will be discussed.

3.2 Fledgling Survival up to Settlement

Great Tits feed their young after fledging for one to three weeks (KLUYVER, 1951; HINDE, 1952; DRENT, 1984). Directly after fledging whole families may move up to two kilometers away from the nesting site. The parents tend to take their family to the area where the male spent the first weeks of his 'outdoor' life (DRENT, 1984). When independent, the young disperse from this point. The first year birds

moult from early July to the end of September. As soon as the moult is completed the males' singing activity increases. Young males try to establish a territory while adult males intensify their defense. The fact that territoriality mainly occurs in a restricted period makes it possible to accurately estimate the number of territory owners and candidates before and after settlement. In some cases further settlement may occur after mortality of territory owners. These data are included in the present analysis. The density of autochthonous juveniles present on 1st September was proportional to fledgling density showing that local survival was not density dependent, in spite of large fluctuations in density between the years (fig. 2). No definite conclusions can be drawn on the density dependence of the immigration rate. As a result the number of first-year birds present on 1st September is roughly proportional to the number of fledglings raised in the area. Thus in this particular case local survival up to the settling stage does not depend on density.

3.3. *Effect of the Density of Adult Males and Candidates on Settlement*

Since we are mainly interested in understanding the individual's chances of settling, the parameter that needs to be explained is the proportion of settlers to candidates.

Fig. 2. Density of autochthonous and immigrant males on September 1st in relation to the local fledgling production in the same area. Density = number per 10 ha. After Drent 1984.

The chance that a candidate (*CAN*) becomes a settler (*SET*) can be estimated as *SET/CAN*. It seems plausible that this chance is negatively affected by both the number of candidates (*CAN*) and the number of resident territorial males (*TER*). In formula:

$$SET/CAN = a - b \cdot CAN - c \cdot TER \quad (1)$$

where *a*, *b* and *c* are constants. The constant term *a* represents the settling chance in the absence of competitors for space. Suppose that the negative effect of the resident territorial birds (*TER*) is negatively affected by the number of candidates (*CAN*) because the resident birds' attention is divided. This would mean that *c* is no longer a constant, but dependent on the number of candidates (*CAN*). Assuming that *c* can be rewritten as:

$$c = c1 - c2 (CAN) \quad (2)$$

Substituting this in formula (1) gives:

$$SET/CAN = a - b \cdot CAN - c1 \cdot TER + c2 \cdot CAN \cdot TER \quad (3)$$

or multiplied by the number of candidates:

$$SET = a \cdot CAN - b \cdot CAN^2 - c1 \cdot TER \cdot CAN + c2 \cdot CAN^2 \cdot TER \quad (4)$$

This model has been fitted to the data with the help of regression analysis where all elements added significantly to explaining the variance in the number of settlers (table 1).

The model explains 96 per cent of the variation in the density of newly settled males. The data were collected in different woods and different years and yet they can be so well explained by the two parameters. This probably indicates that the actual food situation at the moment of settling has little effect. However, the possibility remains that the density of candidates is mainly determined by the food availability. This possibility can be tested by removal experiments. On the basis of the regression model described we can compute for a specific situation, with known densities of both candidates and adult males, the expected density of new territorial males. By removing a certain number of the candidates before territorial activity starts, and subsequently measuring the density of newly settled territorial males, we can test whether the actual number of candidates present or an unknown factor, like food, causes the correlation described above.

A pilot experiment was started in a parklike wood where there were high densities of tits. Nearly half the candidates were removed and settlement measured. The results of this experiment can be seen in table 2. No clear choice can be made as to which causal explanation fits the results. More experiments are needed to judge whether the effect of density of both adults and juveniles is causally involved. In such experiments it is essential to account for dominance in the candidates.

TABLE 1

Multiple regression explaining the number of settled birds/10 ha (*SET*).

$SET = constant + a \cdot CAN + b \cdot CAN^2 + c1 \cdot CAN \cdot TER + c^2 \cdot CAN^2 \cdot TER$				
where:				
<i>constant</i> = - 0.87	(n.s.)	<i>c1</i> = - 0.010	(p < 0.011)	
<i>a</i> = 0.88	(p < 0.001)	<i>c2</i> = 0.008	(p < 0.002)	
<i>b</i> = - 0.052	(p < 0.001)	<i>n</i> = 20	<i>Rsquare</i> = 0.97	

TABLE II

Test of the model from Table 1. Densities are given in birds/10 ha. The removal was undertaken a week before the onset of settlement. For further explanation see text.

	Number of settled birds				
	<i>TER</i>	<i>CAN</i>	<i>Predicted</i>		<i>Found</i>
Density present before removal	18	44			
Density present after removal	18	24	6.3 (1)	1.3 (2)	3.5

(1) Expected on basis of the carrying capacity. (2) Expected on basis of the actual number of *CAN*.

For the time being we conclude that both the number of candidates and the number of adult territorial males largely predict the number of settlers that will be successful, but whether they are involved causally has not yet been proven. The question, as to which factors affect the density of candidates is very important. As DRENT (1984) points out both the level of resources within the area as well as that of the surroundings are crucial in understanding the local density of candidates.

Thus, density dependence in the local survival rate of the male fledglings is not caused by a density dependent survival rate up till territoriality in September. However, territoriality has strong density dependent effects since the birds that are excluded from territoriality show a higher dispersion and eventually will also have lower chances of survival.

3.4. Consequences for Density Dependence

The descriptive model developed above can be used to explore how territoriality and density dependence are interrelated. For different

adult male densities we first explored the relationship between the density of candidates and the number that settled (fig. 3a). If no adult males are present the number of settled candidates is an increasing function of candidate density, but with a decreasing rate of increase. Increasing the density of males that already own a territory both lowers this relationship and eventually even changes the shape from concave to convex.

The consequences for density dependence can best be illustrated by plotting the percentage of candidates that actually settle, as a function of candidate density for different densities of males that previously owned a territory (fig. 3b). The first conclusion is that in all situations adult male territorial density has a negative effect on the settling chances of a candidate. However, the picture is more complicated for the effect of the density of candidates. If the adult male territorial density is below 12 per 10 ha we find, as expected, a negative relationship with the density of candidates. Surprisingly, however, when the adult male density is above 12 males per 10 ha, the model predicts a positive dependence of settling chance on candidate density. Theoretically this is an interesting result, as positive density dependence leads to destabilisation of numbers. However in this case the strong negative effect of adult density on the settling chance will limit the destabilising effect.

A rough estimate of the densities of candidates and territorial males before 1st September for different woods monitored over a number of years can be made and the effect of territoriality on the local survival rates of Great Tits can be predicted. The combinations of densities are given in fig. 4 by a shaded area, superimposed on the lines that give the density-dependent relationships taken from fig. 3b. It becomes apparent that for the Vlieland area we expect negative effects of candidate density on the settling chance, less clear negative effects in most years for the Hoge Veluwe, but positive effects of candidate density in the Liesbos area. Analysis of annual survival rates in both Vlieland and Hoge Veluwe show a negative density dependence of fledging survival on fledgling density (VAN BALEN, 1980; TINBERGEN *et al.*, 1985). Whether in the Liesbos area the expected positive density dependency exists has still to be tested.

3.5. *The Relations between Cost-Benefit and Density Dependence*

Cost benefit analyses have been made of several aspects of territoriality for a number of species. A general model of simultaneous settling is given by DAVIES (1978) and depicted in fig. 5a. Costs are supposed to be an accelerating function of territory size, as a conse-

Fig. 3. a. Density of settled candidates as a function of the initial density of candidates and the density of resident territorial males as predicted by the model in Table I. Density = number per 10 ha.

b. Fraction of the candidates that settled a territory, plotted against the density of candidates and the density of resident territorial males.

Fig. 4. Fraction of the candidates that settled a territory in relation to the number of candidates at five densities of resident territorial males. The shaded areas show the range of densities of candidates and resident territorial males that occur in three different woods (Hoge Veluwe, Vlieland and Liesbos). Estimates for the Hoge Veluwe are based on direct measurements, while those for Vlieland and the Liesbos are less well documented.

quence of the increasing difficulties of defending a large area. The increase in benefit is thought to decline as the territory size increases, because of the increase in effort needed to exploit resources that are widely separated. Maximum net benefit is the point at which benefits minus costs are maximal and can be computed when both the cost and the benefit curves are known.

In the case of simultaneous settling the cost function is expected to increase with the density of potential settlers but the benefit lines does not change. This would mean that the optimal territory size is decreased and more birds can settle. The rate at which territory size decreases as the potential settler densities increase depends on the shapes of both the cost and the benefit curves. In order to find out whether this very simple functional model could predict the observed density-dependent effects, the shape of the curves is specified.

Let us suppose that the cost function is a quadratic one of the form:

$$\text{cost} = a + bx + cx^2 \quad (1)$$

where a , b and c are constants and x is territory size. This function can be thought of as the cost of patrolling the area after settlement in order to keep out remaining potential settlers. Now let us suppose that the additional cost as the density of candidates increases is a function of

Fig. 5. a. Hypothetical cost and benefit functions for territory size during simultaneous settling. The curves indicate costs and benefits as associated to territory size. The vertical line shows at which territory size the net benefit is maximal (after Davies 1978).

b. Simulation of the effect of the number of candidates on optimal territory size. Increasing the number of potential settlers by equal steps increase the cost function (cost functions from right to left) and shifts the optimal territory size with a decreasing rate to smaller values.

the chance of a fight with an intruder. This chance of a fight can be represented by the factor D (density of potential settlers) multiplied by the territory size, assuming that intrusions in this stage of settlement occur all over the territory. The total cost function now becomes:

$$\text{cost} = a + (b + D)x + cx^2 \quad (2)$$

We are now in the position to simulate the different cost functions for different densities. Fig. 5b shows the results of such a simulation. When we compare these cost functions with the benefit function (here the logarithm of the territory size) it becomes apparent that as the density of potential settlers increases the optimal territory size will decrease. At a certain point the net benefit of the territory becomes zero which means that the territorial system breaks down. The rate at which the territory size decreases as the candidate densities increase is entirely determined by the shapes of the cost and the benefit curves, and by the effect that the density of candidates has on the cost function. In our example, it can be shown that territory size prevents some candidates from settling (negative density dependence).

The next question is whether a cost-benefit approach could at least in principle explain why, when the densities of males that already occupy a territory (non-simultaneous settling) is high, positive density dependence may occur. We assume that the benefit curve for the adult males is exactly the same as for the candidates, but that the cost function is different. It is also assumed that the costs for an adult male to keep a territory of a particular size will become less in the course of time because of increased efficiency in patrolling and fighting. However, neighbouring old males also increase their efficiency. They own the adjacent area and will fight as soon as the boundary of their territory is crossed. That means that at the border between two territories the cost function will increase disproportionately sharply, as depicted in fig. 6.

Now let us consider the candidates. They enter the system and increase the cost of territorial defense for the adult males. The territory size that gives adult males the maximum benefit may, when the candidate levels are low, not change because of the shape of the cost function. However, the higher the number of candidates the greater the cost function for the adult male and at a particular point the optimal territory size of the males will become smaller than the actual size. At this point candidates may start to invade the system.

This explanation of positive effects of candidate density on the chance of settling, based on a cost-benefit model, is highly speculative since the shapes of both the cost and the benefit curves are not known. Observations by DRENT (1983, 1984) support the model in that the strong increase in defence activities by resident males as the candidate

Fig. 6. Hypothetical cost function for a resident territorial male (non-simultaneous settling). Increasing the cost function at low densities does not result in a decrease in territory size as optimal territory size does not shrink with intruder pressure due to the discontinuity in the cost function.

densities increase is associated with a greater chance of candidates being able to settle. Although the model is very elegant in theory, it can only be tested when we actually are able to measure cost and benefit curves in a fitness component as a function of territory size. The best chance of being able to test a cost-benefit model occurs in situations where animals set up territories for short periods as occurs with hummingbirds when they set up in feeding territories (PYKE, 1979). The territories of Great Tits are occupied for a lifetime and are important for both feeding and reproduction even when the tits operate outside these boundaries. Experiments manipulating the density of candidates, adults or food may provide both a test of the descriptive model to be developed, and some clues with regard to the shape of the cost and the benefit curves.

4. COSTS AND BENEFITS IN THE BREEDING SEASON

4.1. INTRODUCTION

We have seen in the previous chapter that a cost-benefit analysis may help us to develop specific hypotheses to explain the nature of ter-

itoriality. Tests of these hypotheses should involve detailed measurements of possible costs and benefits, preferably combined with manipulations of territory size. This induced us to look for a system in which we would be able to manipulate the decision under study and measure the effect of manipulation on the associated costs and benefits. We chose to start a manipulation study of brood sizes in Great Tits with the aim of estimating the cost and the benefit functions related to brood size.

The evolution of brood size has been studied in the past by a number of authors inspired by the work of LACK (1954, 1966). In order to unravel the brood size problem it is necessary to know whether there are costs in terms of the future reproduction for the parents, associated with raising a brood. In 1970 Klomp drew attention to the fact that passerines tend to lay fewer eggs than are necessary to produce the maximum number of offspring. This may be because the cost, for the parents, of raising a large brood is high. Recently a number of studies have been made in an attempt to measure these costs (NUR, 1984a; EKMAN & ASKENMO, 1986; TINBERGEN, 1987). We hope to learn from these experiments whether and how parents maximize the number of their offspring in a fluctuating environment.

4.2. *Prospect for Young in Manipulated Broods*

From 1983 onwards broods were manipulated in the Hoge Veluwe. As there are indications that clutch size may be related to individual quality of the parents or their environment (KLUYVER, 1966) we exchanged the young of nests with approximately the same clutch size. When the nestlings were two days old, groups of three nests were selected with the same hatching success. From one we took half the young and added these to a second brood, while the third was kept as a control. Details of the manipulation can be found in TINBERGEN (1987).

Manipulation had strong effects on nestling survival and on their weight at day fourteen of nestling life. In two of the three years the number of nestlings that fledged from enlarged broods was only slightly higher than that of the control group, in the third year however, the enlarged broods produced more young than the control broods (fig. 7a). The weight of the nestlings is a negative function of the manipulated brood size (fig. 7b). Apparently the parents do not adjust their efforts to such an extent that the weights of their young

are unaffected by manipulation. This does not surprise us in the case of the enlarged broods since there may be different factors limiting the ability of the parents to provide the young with food. However, it is less obvious why small broods tend to have heavier young than control

Fig. 7. Number of fledglings (a) and nestling weight at day 14 (b) as a function of brood size just after manipulation.

broods, an indication that fledglings in natural broods in the Hoge Veluwe do not reach their maximum weight. This is a general phenomenon that has been observed in natural broods in a number of species including Great Tit (VAN BALEN, 1973; PERRINS, 1965), Starling (TINBERGEN, 1981), House Martin (BRYANT, 1979) and also in manipulated broods of for instance the Blue Tit (NUR, 1984b). These results indicate that there is a trade-off for the parents between the number of young that they raise and average nestling weight. The question is why the parents chose to raise a higher number of young with a lower average weight. The answer must lie in the relationship between nestling weight and the prospects of both nestlings and parents.

Descriptive data indicate that nestling weight is related to the chance that an individual nestling will become a member of next years breeding population (fig. 8). As recruitment rates are strongly affected by the abundance of food in winter (VAN BALEN, 1980), separate curves were drawn for years with a high and a low seed index. The curves suggest that recruitment rate is a positive function of nestling weight up to weights of ca. sixteen gram, and after that it is more or less constant. The same kind of relationship was found by DRENT (1983, 1984). Both the chance for a male of surviving until September and the chance of getting a territory thereafter were positively related to nestling weight.

We can calculate from such data the expected number of recruits per first brood based on the weight of the individual nestlings in the manipulated broods. This shows an optimum curve relating the expected number of recruits to the initial brood size (fig. 9). The optimum brood size is a trade-off between the weight of the individual nestling and the number of fledglings that can be produced. It is higher than the actual average brood size measured in the area. The fact that there is a discrepancy between the brood size 'chosen' by the birds and the brood size predicted as being the most productive, may be explained in different ways. One possible reason is that the estimate of the recruitment rate as a function of nestling weight based on non-experimental data is biased, for instance by qualitative differences between individuals that are related to nestling weight. Better estimates will eventually be available based on experimentally manipulated brood sizes.

Another reason for the discrepancy between predicted and actual brood size is that there may be a cost, as suggested above, in terms of future performance of the parents, related to brood size. This cost will be discussed in the next section.

Fig. 8. Local recruitment rate as a function of nestling weight, separately for years with a high seed index and for years with a low seed index. To model optimal brood size an average curve was computed from these two curves, weighed for the frequency of years with a high and a low seed index.

4.3. *Prospects for Parents in Relation to their Current Reproduction*

In recent years considerable effort has been made to try to find out whether there is a cost to the parent birds in terms of future reproductive output, associated with their current level of reproduction. Basically we do not know which aspects of the parental effort are likely to affect their future reproduction and thus can be taken as parental investment. A final answer to this question can only be given based on experiments manipulating parental effort and measuring the future reproduction of these manipulated birds. Non-experimental data can however indicate whether or not effects can be expected. We will discuss here some non-experimental data before we return to the cost-benefit analysis of brood-size in detail.

Fig. 9. Expected number of local recruits per first brood as a function of initial brood size. The values are estimated on basis of the relationship between manipulated brood size and both the nestling weight and nestling mortality. Non-experimental data were used to estimate the recruitment rate as a function nestling weight as shown in fig. 8. Arrow indicates optimal brood size, bar indicates most frequently observed brood size, computed from 12 years' data.

4.3.1. Evidence from the Long-Term Monitoring Study

Since, thanks to the long-term monitoring studies, our group has data available on several populations of Great Tits, we are able to look for correlations between different aspects of the breeding cycle and future reproductive success. This technique has theoretical problems, as has been pointed out by a number of authors (VAN NOORDWIJK & DE JONG, 1986; NUR, 1984a; TINBERGEN, 1987; DEN BOER-HAZEWINDEL, 1987). It cannot be regarded as proof of the existence of costs of reproduction as quality of birds may covary with reproductive effort. However, it can give some hint as to what aspects of the breeding cycle may be important and how we should set up the experiments.

In a recent reanalysis of the data collected by Kluyver and van Balen on Vlieland a correlation was found between the number of fledglings produced annually and the parents' chance of surviving locally (TINBERGEN *et al.*, 1985) provided that the winter seed food index was low (fig. 10). This effect was so strong that per extra young produced parental survival to the next breeding season was estimated

to be about five percent lower. However, the selection pressure was absent in the years with a high seed index in the intervening winter. The costs of reproduction are possibly greatly dependent on additional factors, which may, to a certain extent, explain why some authors observe it and others do not. Recent work of EKMAN & ASKENMO (1986) shows that Willow Tits that loose their mate and do not reproduce have a much better survival chance than the members of their group that reproduced. Analysis of non-experimental data of other populations under study showed a positive relationship between the production of fledglings and the local survival rate (*i.e.* whether or not a second brood is produced, DEN BOER-HAZEWINDEL, 1987).

Fig. 10. Annual local recovery rates of Great Tits on Vlieland in relation to the number of fledglings produced in the preceding year, for years with a high seed index (a) and years with a low seed index (b). From TINBERGEN *et al.* (1985).

The timing of the breeding season of individual birds seems crucial to their lifetime reproductive success, as young that have hatched early tend to have higher chances of being recruited (KLUYVER, 1951; PERRINS, 1965). Why some tits start laying later than others has received a lot of attention. PERRINS (1965) argued that the food necessary for the female to produce her eggs may be the limiting factor. Experiments by KÄLLANDER (1974) showed that extra insect food supplied before egg laying may advance the laying date by one week, supporting Perrins' hypothesis. However observations on the Hoge Veluwe revealed that in some years the Great Tits do lay their eggs until the clutch is completed but do not start incubation until up to a week later. MERTENS (1980) found that females tend to do this in times with low ambient temperatures. Only very adverse circumstances cause the birds occasionally to interrupt laying. This leads us to believe that in the Hoge Veluwe situation not so much the production of the eggs, but especially the incubation period may be the bottleneck in the timing of the breeding cycle. MERTENS (1987) therefore started a program to measure the energy content of female Great Tits in different phases of the breeding cycle in order to find out whether ambient temperature would affect energy reserves. The following is a discussion of the relationship between ambient temperature and energy content of the female during the incubation period.

In order to estimate the relationship between ambient temperature and energy contents at the end of the incubation period, female Great Tits were collected just after their first egg hatched. Over a period of three years 21 birds have been collected and analysed. Both the lipid and the protein content were determined.

The average ambient temperature during a period of eleven days preceding the capture of each bird was calculated, using the temperature values from the nearby weather station Deelen.

The results (fig. 11) show that the temperature strongly affected the lipid content of the female but hardly affected her protein content. As ambient temperatures tend to be lower early in the breeding season, the temperature effect on the lipid content is an indication that there is a cost associated with early laying. Whether clutch size has an additional effect remains to be studied.

This suggests that the incubation period may act as a bottleneck period in the reproductive cycle, which has been suggested before by BIEBACH (1977). The reason may be that the time available to the female for foraging is greatly reduced in the incubation period. Temperature affects the time that the female has to spend on the eggs (HAFTORN, 1985; DRENT *et al.*, 1985) and possibly also the availability of food. Both these factors can lead to the observed lowered energy reserve of the female.

Fig. 11. Energy content of female Great Tits at hatching of their clutch as a function of the mean temperature over the 11 preceding days. Triangles denote protein energy content while circles denote lipid content. From MERTENS (1987).

Whether this lowered energy reserve affects the future reproductive output of the female is not known but it is likely that it has adverse effects on the ability to feed the young when they hatch.

4.3.2. *Experimental Evidence*

Returning to the brood size manipulations in the Hoge Veluwe area we will now trace the effects of manipulation on the future reproduction of the parents. Brood size manipulations had a strong effect on the probability that a female would produce a second clutch (fig. 12, TINBERGEN, 1987). The general form of this relationship seems to be concave down, indicating a non-linear effect. Enlarging the brood decreases the probability of a second clutch much more than a reduction of the brood increases this probability.

Thus in the Great Tit there is a cost associated to the size of the brood in terms of the future reproduction of the parents. The number of breeding attempts is lowered if more nestlings than 'planned' were in the nest during the first brood.

Fig. 12. Percentage of second broods produced per experimental category and per year, plotted against the initial number of nestlings in the first brood. From TINBERGEN (1987).

Fig. 13. Expected number of local recruits produced per pair per year (open circles) and for first broods only (solid circles) as a function of the initial size of the first brood. Arrows indicate the optimal first brood sizes for maximal annual production (left) and for maximal first brood production (right).

It is possible to calculate how this cost would affect the optimal size of the first clutch. The expected number of local recruits from a second clutch, multiplied by the chance that a second clutch is produced as a function of initial brood size, should be added to the expected number of recruits computed for the first brood nestlings only (section 4.2). As can be seen (fig. 13) this shifts the optimal brood size well to the left, but it still does not quite correspond to the average brood size found in this population. This may be related to the fact that second brood young tend to disperse more than first brood young which lowers the optimal clutch size.

The mechanism by which the production of second broods is affected is of special interest. Analysis of the weights of both male and female while tending young show that these are not affected by the manipulation. Thus the hypothesis that the condition of the parents is affected by manipulation does not hold, for this population. Detailed analysis shows that there is a relationship between the number of nestlings and their condition on the one hand and the inter-brood interval on the other (TINBERGEN, 1987). Similar manipulation experiments were done by Slagsvold (1984) who, however, removed the nestlings just before fledging and found a much less pronounced relationship between brood size at day 15 and the inter-brood interval than we did (fig. 14). This suggests that the parents face a trade-off between tending the fledglings of the first brood and starting a second. Presumably the value of the first brood increases the longer the parents tend it, but with a decreasing rate of increase. At the same time the expected value of a second clutch will decrease as the season progresses. At the point where the expected increase from tending the first brood young becomes larger than the expected pay off from a second clutch the parents should decide not to produce a second clutch. In these circumstances producing too large a first clutch may reduce the future reproductive output of the parents without affecting their condition. Whether the survival of the parents is affected by the production of a second brood has yet to be determined.

4.3.3. *Availability of Food and the Future Reproductive Value*

In order to estimate the effects of additional food, an experiment was conducted in which parents tending their young were supplied with extra food (DEN BOER-HAZEWINDEL, 1987). The idea behind this experiment was that the 'work load' of the parent might be associated with options in the future in terms of survival and or reproduction. To achieve a lower work load a food cup was attached inside the nestbox of half the pairs while the first brood young were in the nest. Observa-

Fig. 14. Scatter diagram of the interval between hatching date of the first brood and the laying date of the first egg of the second clutch, plotted against the number of young in the nest. Black dots indicate intervals after removal of nestlings on day 15 (data: Slagsvold pers. comm., $y = 20.2 + 0.15x$). Open circles indicate intervals for the Hoge Veluwe 1985 - where nestlings were not removed - plotted against the number of nestlings on day 14 ($y = 13.7 + 0.95x$). From TINBERGEN (1987).

tions revealed that the parents would take food from the cup and feed it to the young. This reduced the feeding frequency considerably (table 3) and presumably also their feeding effort. The experiments were done in two successive seasons in a 'rich' oak wood (Oosterhout). In the first year fed and non-fed pairs were randomly assigned within the wood while in the second season the fed nestboxes were in one part of the wood and the non-fed in another, to maximize differences in possible depletion effects of the natural food. Body weights of both the parents and the young were significantly higher in the fed group. Nevertheless there appeared to be no effect on the probability that the parents would start a second clutch nor on the local survival rate as estimated from the recaptures in the next breeding season (table 3).

These data suggest that lessening the parents feeding effort when tending their young does not increase their future reproductive value and agrees with the result that decreasing brood size does not affect the future reproduction of the parents.

TABLE III

The effect of extra food on feeding frequency, the probability of making a second clutch and parental local survival over two years (1979, 1980) in Oosterhout, an oak wood. Visits/young/24h were tested with a sign test, as data were collected on the same day for 3 fed and 3 non-fed pairs. Per cent second broods and adult survival were tested in a two by two table.

	<i>Fed</i>		<i>Non-fed</i>		
	$\bar{x}$	<i>n</i>	$\bar{x}$	<i>n</i>	
Visits/young/24h	30.0	(14)	48.9	(14)	$p < 0.001$
Per cent second broods	21.7	(46)	28.8	(72)	n.s.
Per cent adult survival	54	(46)	54	(72)	n.s.

5. CONCLUDING REMARKS

Life history theory concentrates on explaining the lifetime reproductive success of individual animals (STEARNS, 1976). To understand the selection pressures at work it is essential that data are collected on the lifetime reproduction of individual birds in nature in relation to particular aspects of their choices or strategies. Such a study is possible in wild populations when detailed life history data are available over a number of generations. The Dutch and the English population studies of the Great Tit are such studies. Recently detailed descriptions of the variations in lifetime reproductive success of Great Tits both in Holland and in England were made. General conclusions from this work are that variation in recruitment rate of the fledglings and variation in the life span of the adult are the main factors contributing to the variation in lifetime reproductive success.

This leaves us with the question what factors determine recruitment rate and adult life span. These questions are as old as population dynamics itself, be it that they emerge from a different type of analysis. The main difference is that life history theory takes the individual as the unit, while population dynamics tends to focus on (sub)populations as units, and the year, or part of it, as a unit of time. Both variations between individuals and variation in time are of great importance. For further progress, it is necessary to conduct experiments that manipulate a particular factor and measure how this factor affects lifetime reproductive success. Since not all elements of the life history of an individual can be manipulated easily one should select specific situations in which experiments can be done and fitness components can be measured. The cost-benefit analysis of brood size

is an example, since it is possible to relate choices, like the one on brood size, directly to reproductive output. This opens the possibility to tackle for instance the question of the effect of individual differences on lifetime reproductive success. Do individuals actually differ in the number of nestlings they can raise, and is this difference explained by the local circumstances or do we have to allow for inherent differences between individuals? Is the optimal solution different for different individuals?

The same kinds of questions can be asked about territoriality, but the possibilities for experimental manipulation are far less obvious. However, territoriality is of prime importance in understanding the life history of the Great Tit, so a great effort may be worthwhile.

Research will have to proceed in two ways. Detailed experimental analysis of part of the system may lead to verification of theoretically interesting points, while description, especially in those cases where experiments are impossible, must lead us to a general understanding of the life history of the species under study.

The reproductive value of an individual Great Tit will depend on its physiological and behavioural capacities to survive and reproduce. Some of these capacities can be measured by decisions taken by individual birds. Here follows a summary of the decisions that we think are of prime importance for the Great Tit during its annual cycle and we suggest experiments that may show factors affecting the outcome of these decisions.

Firstly the decision on the timing of breeding and on clutch size. We hope to unravel which factors affect the decisions that the parents take in relation to the size of their brood by making detailed measurements during the nestling stage, combined with experimental manipulation. Then we hope to trace how choices of the parents during the nestling stage affect the development of the nestlings, and whether this in turn has effects on the nestlings chances of being recruited. At present there are clear signs that nestling weight on day 14 is related to their chances of surviving the first year, and it may even be the case that their own production of recruits is related to their weight as a nestling. Yet nestling weight explains only a small part of the variation in fledgling survival.

The role of the parents is of importance as they take their brood with them and their experience may be crucial in finding good sites and therefore guiding their helpless young to independence. Parents that have to spend a lot of time with their young may have reduced chances of starting a second clutch, and the experiments with additional food during the nestling phase indicate that extra food reduces the interval between the first and the second clutch. The moment that

parents decide to wean the young can be seen as a trade-off between a reduced value of a potential second clutch as the season advances and a increase in the prospects of the first brood young as they are tended longer. Here the important role of timing becomes clear, and experiments manipulating the timing of breeding should be undertaken.

As the nestlings become independent they will roam the area and we believe that food plays an important role in their spatial distribution. Experiments to manipulate the food supply for first year Great Tits in the period between the breeding season and the onset of autumn territoriality will be crucial to establish causality. Dominance hierarchies develop, which determine who is to have first access to resources such as food and space. The factors that are involved in determining a dominant position are important in understanding population dynamics as the dominant birds will be the ones that can settle.

As the territorial strife is over, birds that were not successful have the choice of staying put and waiting until a vacancy occurs, or they will disperse in the hope of finding less populated areas. The cost-benefit approach to this decision will be very interesting. It will be essential to follow individuals over greater distances than has been the case up till now. The outcome of the different dispersal strategies will depend on the winter weather, the beech crop and other winter foods such as those supplied by humans. In harsh winters territorial males may be forced to leave a wood for longer periods, thereby running the risk of losing their territories. Additional feeding in years when the beech crop is low will make it possible for the male to maintain his strategy of staying in his own territory. Long term effects on the composition of the population are bound to occur, and the variation in the environment will here also be of great importance not only in determining numbers, but also in determining the composition of the population.

Finally a new wave of territorial behaviour may occur as in spring the birds that left the area, return in order to try and get a territory or a mate, both essential resources of the successful tit. Once established and mated they will again have to 'decide' on laying date and clutch size.

Constructing optimality models for all these decisions will be an enormous task but may enable us to make predictions on how birds are likely to behave in particular situations. By testing these predictions we can test our knowledge about the factors determining behaviour. The final aim should be to integrate effects of density and competition into these models. If we succeed in this we may be able to predict general trends in animal numbers from models based on behaviour of the individual.

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